Role of Visual Hemifields
in
Processing and Storage
of
Motion Information

By

Sharavanan Ganesan

THESIS

In partial satisfaction of the requirements for the degree of

Master of Science

in

Physiological Optics

Presented to the

Graduate Faculty

of the

College of Optometry

University of Houston

December, 2016

Approved:

_____

Dr. Haluk Öğmen, Ph.D. (Chair)

_____

Dr. Laura J. Frishman, Ph.D. (Co-Chair)

_____

Dr. Harold E. Bedell, Ph.D.

Committee in Charge

ACKNOWLEDGEMENT

Foremost, I would like to express my sincere gratitude to my advisor Dr. Haluk Öğmen for the continuous support of my M.S. study and research, for his patience, motivation, and immense knowledge. His guidance helped me in all the time of research and writing of this thesis. I could not have imagined having a better advisor and mentor.

I owe special thanks to Dr. Laura Frishman, co-chair, for her great support and for her enormous help and encouragement throughout the graduate studies and throughout the development of the thesis.

Besides my advisor, I would like to thank Dr. Harold Bedell, committee in charge, for his help, encouragement, insightful comments, and hard questions. I am extremely grateful for his wisdom, understanding, and patience to help me complete my degree.

My sincere thanks also goes to all graduate faculty for helping me in understanding enigmatic vision science in an easy way. I would like to express my special thanks to Ms. Hope Queener for her inspiration and help.

This work would not have been possible without my observers; I am indebted to them.

Last but not the least, I would like to thank my family: My parents, Uma and Ganesan, receive my deepest gratitude and love for their dedication and support that provided the foundation for this work.

DEDICATION

To my parents and sister, for making it possible to embark on this journey.

To my teachers, for making it possible to conclude it.

Role of Visual Hemifields
in
Processing and Storage
of
Motion Information

By

Sharavanan Ganesan

An abstract of a Thesis

Presented to

The Faculty of the College of Optometry

University of Houston

In partial fulfillment

Of the requirements for the degree

Master of Science

In

Physiological Optics

By

Sharavanan Ganesan

December 2016

ABSTRACT

PURPOSE: Studies on motion processing using multiple-object tracking indicates that the bottleneck of information processing occurs at the visual-short term memory (VSTM) stage. In contrast, recent studies reported the bottleneck to occur prior to VSTM at the stimulus encoding stage. Performance in motion processing is greatly influenced by attention to the task. On the other hand, studies on attention, e.g. Alvarez and Cavanagh (2005), suggest that there are partial or independent resources for attention across each visual hemifield. The purpose of this study was to investigate, using a cross-cuing approach, whether attentional resources are partial or independent in motion processing across different memory stages.

METHODS: In the first (N=9) and second experiments (N=8) observers reported the direction of motion of a target through a partial-report technique where the target's terminal position was cued. The targets were distributed equally and either confined to one hemifield (unilateral) or both visual hemifields (bilateral). The cue was presented either immediately after the stimulus presentation, or with a delay that ranged from 50 to 3000 ms to investigate the processing of motion across stimulus encoding, sensory, and VSTM stages. A third experiment (N=8) was designed to replicate the findings of Alvarez and Cavanagh.

RESULTS: At the stimulus encoding stage, performance gradually declined (30%) as a function of set size but there was no statistical significance between the unilateral and bilateral conditions. At the sensory memory and the VSTM stages, the main effect on performance was due to set size. Again, there was no effect on performance due to the

visual-field location of the targets. In the third experiment, performance in the bilateral and unilateral conditions was similar and with no statistically significant difference.

CONCLUSIONS: I did not find any evidence for independent attentional resources for each hemifield in processing the direction of stimulus motion. The results of this study support findings of previous studies that the bottleneck of motion processing occurs prior to VSTM, at the stimulus-encoding stage.

Table of Contents

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

General Introduction

1.1 Introduction:

Understanding the human visual system's ability to process the information that falls on the retina is a great challenge to vision scientists. This processing of information involves memory since, to make sense of the stimulus received at a given instant, we need to put it into the context of what was received and analyzed previously. Human memory involves three components following the stimulus encoding stage viz., sensory memory or iconic memory, visual short-term memory (VSTM), and long-term memory (LTM) (Sperling, 1960; Cowan, 2001). In a real life scenario, different objects with different features that undergo different actions are perceived simultaneously. This implies that the stimuli falling at different retinotopic loci are processed in parallel. This parallel processing occurs at early stages of stimulus processing; hence, sensory memory is expected to have a large capacity. The contents of sensory memory are then transferred to later memory components and the information that is transferred depends on the decay constant for each stage of memory and the selection and filtering functions of attention that happen during the course of processing. Multiple-object and/or multiple-identity tracking paradigms are widely used in studies of motion processing, memory, and attention. The preferred stimulus used for these types of studies is multiple dots moving in random trajectories from random locations.

The traditional analogy given for information processing and stages of memory is a "leaky hourglass." According to this analogy, the major bottleneck in information processing occurs at the visual short-term memory stage, represented as the narrow central part of the hourglass, whereas the very large capacity of iconic memory and LTM comprise the wider top and bottom of the hourglass (Cowan, 2001; Alvarez and

Cavanagh, 2004; Fukuda et al., 2010). On the other hand, recent studies (Ogmen et al., 2013; Huynh et al., 2015) reported significant information loss at the stages of stimulus encoding and sensory memory prior to VSTM. The results suggest a limited capacity at the stimulus encoding and sensory memory stages, which were thought previously to have large capacity. The capacity limits at the stimulus-encoding stage are consistent across different stimulus dimensions, like motion and color. The commonality among the previous studies and the recent studies from Ögmen's lab is the role of attention. Attention is believed to be involved in target selection; this filtering function of attention is considered to occur at the sensory memory stage.

On the other hand, studies on attention have raised the possibility of completely or partially independent attentional resources for the left and right visual hemifields during multiple-object and multiple-identity tracking paradigms (Luck et al, 1989; Alvarez and Cavanagh, 2005; Hudson et al., 2012). In addition, with respect to memory and attention, VSTM has been reported to have a bilateral hemifield advantage (Delvenne, 2005; Delvenne et al., 2011; Delvenne and Holt, 2012). In other words, the performance of the observers is better when the targets were distributed across hemifields than within one hemifield. As mentioned above, multiple object tracking (MOT) tasks are widely used to study the processing and storage of motion information, as influenced by attention and memory. In most studies, MOT targets were presented in random locations in the visual field. It would be interesting to find the contribution of each hemifield and the limit within each hemifield for processing and storing motion information, especially direction of motion, both in sensory memory and VSTM. To the best of our knowledge, no study

has probed the contribution of the two hemifields in processing and storing motion information that is available from stimulus encoding, in sensory memory and STM.

1.2. Memory and Motion processing:

Visual memory can be classified into high capacity sensory memory that has a brief duration and short term visual memory that last for a few seconds with limited storage capability (Philips, 1974). Sperling (1960) used a partial report technique to understand iconic memory. In his study, the observers were asked to report letters presented for a brief duration (15 to 500 ms). Observers were able to report a maximum of four letters. To determine whether the immediate memory capacity was this limited, the author designed another experiment in which observers were asked to report only a part of a displayed array of letters containing 6, 8, 9, or 12 symbols that were shown for a short duration. The part of the display that observers reported was signaled by an auditory cue. The accuracy in this-partial report technique was better than the previous whole-report technique. The data indicated that observers had access to as many as 9 letters from a 12 letter array, corresponding to an accuracy of 76% in the case of the partial-report technique. The accuracy dropped as a function of cue-delay time, reaching the accuracy estimated using the whole-report technique after a delay of 1s. According to the author, a large amount of visual information remains available for a short period of time in sensory or iconic memory.

Information estimated using the partial report task for iconic memory involves two processes of transfer; the first process is selective (Sperling, 1960) and the second is a non-selective process (Averbach and Coriell, 1961, cited in Gegenfurtner and Sperling, 1993). During the time between the disappearance of the stimulus and the appearance of

the cue, information transfer of items occurs from iconic memory to visual short-term memory. This information transfer is non-selective with reference to the cue. However, for short cue delays, this non-selective transfer is absent, selective transfer of the cued information occurs. The balance between the two types of transfer depends on the retinal location, the subject's attentional state, and the cue delay (Gegenfurtner and Sperling, 1993).

Demkiw and Michaels (1976) studied whether the information involving the direction of motion and position of a moving target is stored in iconic memory. They carried out two experiments. In the first experiment, they wanted to determine if there is any relationship between the partial-report and whole-report techniques for reporting direction of motion. The results of this experiment (N=4) indicate that direction-of-motion information is represented in iconic memory. This was confirmed by comparing the performance for reporting the direction of motion using a whole-report technique to the performance for reporting the location of the moving objects by cueing the direction of motion. The performance in the partial-report technique was better by a factor of 2 when compared with the whole-report technique across all blocks.

In the second experiment, the authors used different cue delays of 0, 500, and 1000 ms to get an estimate of how iconic memory decays over time. The results of the experiment indicate that the percentage correct for cue delays of 0, 500, and 1000 ms, estimated using the partial report technique, were 76%, 70%, and 66%, respectively. There was no difference in the performance using the whole-report technique as a function of time. However, there was more than a twofold difference between the performance estimated using partial report and performance estimated using whole report as a function of the cue

delay. The results of this study suggests that information about the direction of motion is available during sensory memory and better estimated using partial-report technique.

Magnussen and Greenlee (1991, 1992, 1996) investigated the role of short-term memory in visual motion storage. Short-term memory for spatial frequency discrimination was assessed by two-alternative-forced-choice testing by varying the inter-stimulus interval (ISI) between two gratings. The ISIs that were used ranged from 1-30 seconds. There was a short-term retention of spatial frequency information for a stationary grating and for the velocity of a moving grating for all the ISIs tested (up to 30s). In addition, this short-term retention of information was seen for all spatial frequencies ranging from 5-20 cycle/deg. The addition of a mask during the interstimulus interval affected performance, which suggests the masking stimulus affects short-term memory storage.

When the subject's task was to discriminate the difference between two gratings based on spatial frequency, masking caused an increase in threshold when there was a change in spatial frequency between the test and the mask but not when there was a change in grating orientation. The authors postulated a model wherein the spatial and temporal dimensions of a stimulus are encoded in parallel representations. These representations, or memory stores, are organized in a way such that they allow interaction within a dimension but not between dimensions (Magnussen and Greenlee, 1991 & 1996).

In a study by Blake and colleagues (1997), the authors carried out three different techniques to understand how motion information for random-dot stimuli is stored and recalled across different delay intervals. In the first, "point and click," technique the authors used coherently moving dots that were shown for 1 second. After various delays ranging from 0 to 8 s (0, 1, 2, 4, and 8 s), the observers were asked to recall the direction

of motion and to use a mouse cursor to report the direction of motion on the circumference of a 3-deg diameter circle. The absolute error between the actual and the reported direction motion, calculated for the 8 observers, did not differ much as a function of delay. There was also no statistically significant difference in the error magnitude across different delays as the subjects could recall the direction of motion that was presented. The authors also were interested to study if extra-retinal eye-movement information is used in judging the direction the motion. To rule out the contribution of eye-movement cues, the observers were presented with a fixation stimulus that moved across the screen randomly. The results indicate that there was no statistically significant difference in the errors across different delay intervals. From this experiment the authors conclude that there was no significant eye-movement contribution to the accuracy of motion information stored in memory.

The authors checked the consistency of the results from the previous experiments using the psychophysical technique of forced choice. The observers were asked to recall if the direction of the random-dot motion was either clockwise or counter clockwise with respect to the previous sequence. This was done after different delays of 0, 4, and 8 seconds. The authors found that the slopes of the psychometric function don't differ across the different delays and that the results were consistent for all of the observers with those of the point-and-click experiments described above. Together, these experiments reveal that there is no decay for at least 8 seconds in the accuracy of memory for a single motion direction.

Blake and colleagues (1997) studied how the decay in accuracy in judging the direction of motion changes when targets with multiple motion directions are shown. In this full-

report-technique experiment, the observers were presented with multiple random dot patches with different set sizes of 3, 5, 7, and 9. The task of the observers was to remember the direction of all the random dot patches for memory intervals of 0, 10, and 30 seconds. The interval between each successive random dot patch was 750 ms. In the whole report technique, the observers were asked to report the directions of motion in the order in which they were displayed. The results of this experiment indicate that whole-report accuracy dropped with an increase in the number of motion directions or the number of moving random-dot patches, but this deterioration didn't change across different memory intervals. In other words, performance dropped when there was an increase in the number of motion directions to remember but not as a function of the memory interval.

Blake et al. (1997) also did a similar experiment using partial-report technique. Again, the performance was more dependent on the number of directions to be recalled than on the delay interval. These results are contradictory to those obtained in other studies, in which performance decayed as a function of the delay interval (Shooner et al., 2010; Ogmen et al., 2013; Duong et al., submitted). Blake et al. (1997) attributed this difference to the fact that observers might be banking on short-term memory instead of iconic memory. Blake et al. (1997) concluded that the memory for motion does not decay even if the subjects are asked to remember the degree of coherence in a random dot stimulus.

Pasternak and Zaksas (2003) used a masking paradigm to investigate how information about motion objects, like speed, direction, and size, are stored in memory. A random-dot stimulus was presented, followed by a memory mask, to two trained macaques. Direction thresholds were estimated using a staircase procedure. The results showed the mask had a greater effect on performance when the mask was presented at the exact location of the test stimulus with a mask delay of 100-200 ms, and when the size and speed of the mask matched the target to be remembered. The results of this study specify the maskable properties of sensory memory. On the other hand, a maskable stimulus does not have any influence on performance when the masks occurs during the short-term memory retention period (Magnussen and Greenlee, 1991, 1992, & 1996).

Bradley and Pearson (2012) investigated how low-level features such as color, orientation, and motion are stored in iconic and visual working memory. The authors used three types of stimuli to test color, motion, and orientation across different cue delays. For the orientation and motion tasks, the observer reported whether the cued target had a more clock wise or counter clockwise orientation or direction of motion than the test target. For the color task, observers' were asked to compare whether the cued stimulus was more green or more red with respect to the test stimulus. The thresholds for all three tasks were calculated by a forced choice technique. In the first experiment (N=5), the authors used Gabor patches to test orientation, uniform hue patches that varied from red to green to test color information, and random dot kinetograms to test motion. The cue delays used by the authors were 0, 100, 200, 300, 400, 500, 600, 700, 1000, 2000, 3000, 4000, and 6000 ms. The results of the first experiment indicate that there was an exponential decay of performance as a function of cue delay for color, motion, and orientation. A rapid drop

in the performance was found mainly for the cue delays between 0 and 1000 ms, indicating the operation of iconic memory. However, the changes in performance during this time interval suggested that iconic memory might hold less information about motion direction when compared with color and orientation. At cue delays more than 2 seconds, performance was at the chance level for all tasks, suggesting that visual short-term is greatly influenced by attention-demanding tasks, unlike iconic memory.

Bradley and Pearson (2012) wanted to understand which form of memory influences the performance at 1000 ms. To do so, they compared the performance for color, motion, and orientation in two conditions, one involving a non-attention task in the form of a blank interval and the other involving an attention task in the form of a distractor stimulus that was presented rapidly during the delay. The results of this experiment indicate that the performance for all three features, i.e. color, motion, and orientation, is based on visual short-term memory at 1 s and longer and is greatly influenced by an attentional distractor. As in the authors' first experiment, the observers' performance on the motion task with no distractor indicates that less motion information is stored after 1 s, when compared with the features of color and orientation. In a third experiment, the authors were interested to find whether iconic memory and visual short-term memory are influenced by the retinotopic location of the stimulus. This was tested by presenting the orientation stimulus either at the same location as the cue, at opposite location as the cue, or at the center of the monitor and the subjects performance was assessed for different cue delays. The results of this experiment indicate that visual memory is greatly influenced by the retinotopic location of the stimulus. Performance was better when the test stimulus was presented at the same location as the cued stimulus than when the test stimulus and the

cue were shown at different retinotopic locations. From these experiments, the amount of information stored in iconic memory was determined to be less for motion than for color or orientation stimuli.

1.3. Visual Working Memory – The bottleneck?

Pylyshyn & Storm (1988) reported that the maximum number of objects that could be tracked in a multiple-object tracking paradigm in the presence of distractors is four or five items. Luck and Vogel (1997) asked their observers to detect supra-threshold changes in colored squares that were presented after a brief retention period of 900 ms. The subject's performance gradually decreased when set size was increased. This result was consistent when the observers had to judge a single feature like color or multiple features like color and orientation. The result of these studies indicate that visual working memory has a capacity limit of 4 approximately items. Similarly, Zhang and Luck (2008) found the capacity of working memory is discrete but Bays et al. (2009) concluded that the visual working memory capacity is allotted as a single resource that is shared depending upon the attention allotted.

According to Cowan (2001), the bottleneck of visual processing lies in visual short-term memory, which is contrast to recent studies (Ogmen et al., 2013; Huynh et al., 2015). The limit for visual short term memory storage capacity is approximately four items if the items are attended. However, performance and the estimated storage capacity drops if the items are not attended (Cowan, 2001; Awh et al., 2006). On the other hand, Bradley and Pearson (2012) reported that visual memory can hold information about 10 items of low level features for over 1s.

In contrast, Tripathy and Barrett (2004) found that the observers were unable to track more than one change in motion trajectory in a multiple-object paradigm. In their

experiment, a typical stimulus consisted of one target and many distractor trajectories. The target moved from left to right along a bi-linear trajectory with subtle deviation midway through the trajectory. On the other hand, the distractors moved smoothly from the left half of the screen to the right half. Observers were not informed which trajectory was the target. The task of the observers was to detect the smallest deviation that they could perceive in the target trajectory. The threshold deviation increased rapidly as the number of distractor trajectories was increased.

Narasimhan and colleagues (2009) modified the procedure from the study by Tripathy and Barrett (2004) to understand the role of attention and memory in tracking multiple moving objects. The performance of the subjects in Tripathy and Barrett (2004) study was poor because the target trajectory was not attended; the task of the subjects was to detect deviations of a moving trajectory. The subjects were asked to track the target trajectory in the presence of distractors through out the trial. This might influence the performance as the target trajectory might have not been tracked resulting in poor performance. To overcome this limitation (Narasimhan and colleagues.2009), the target was only one trajectory that was shown in the first half of the trial or second half of the trial. This modification might facilitate the target monitoring as well target recall. In addition to the modification above, the target used by Narasimhan and colleagues (2009) changed color when it reached the vertical midline unlike distractor trajectories. In their experiments, the observers were asked to detect the deviation of the motion trajectories in the presence of distractors. The performance gradually decreased as the number of distractor trajectories were increased. They found that the main factor that limits human performance was the presence of trajectory traces in the sensory memory. Similarly,

Shooner et al. (2010) suggested that sensory memory retains information about motion for a limited span of time. In addition, Shooner et al. suggested that motion performance does not depend on the stimulus duration, but rather on the set size of moving objects. The results of the Shooner study showed that the number of moving objects that can be tracked simultaneously is limited to four or five items. The maximum representation that working memory can hold is still under debate (Fukuda et al., 2010).

Fundamental stimulus features like size, orientation, speed and direction of a motion stimulus can be retained in working memory without much of loss of information. The loss of information or the retention of information depends on the type of stimulus attributes that are stored. For example, the rate of loss of information was more for stimulus attributes like contrast, Vernier offset, texture, and direction of motion whereas the rate of loss of information was less for stimulus attributes like speed of motion, spatial frequency, and orientation (Pasternak and Greenlee, 2005). This indicates that different processing mechanisms and different storage mechanisms exist for different stimulus features. The processing in VSTM undergoes two separate stages: an early encoding stage that can be influenced by masking stimulus and a robust later stage. Prefrontal cortex plays an important role in sensory working memory. Depending on the stimulus features used, imaging studies found activation of cortical areas MT and MST (motion) or V4 (color) Studies on subjects with focal brain damage or structural lesions indicates that these structures also are involved in the processing and retention of information (Pasternak and Greenlee, 2005).

In a study by Luck et al (1997), memory capacity was estimated based on the number of objects, rather than on the number of object features, that were stored. Subsequently, Alvarez and Cavanagh (2004) investigated the storage capacity of visual short-term memory by probing whether the information stored is based on the number of objects or the visual details of those objects. Alvarez and Cavanagh also tried to estimate the total number of objects or total number of features stored. To estimate this, the authors used different classes of objects like shaded cubes, shaded polygons, Chinese characters, letters, colored objects, and line drawings. Visual search rate was estimated by taking the slope of the line relating reaction time for target-present conditions to the number of objects presented. The observers were presented with one or more targets for 500ms. After 900 ms, an array of 4 or 8 or 12 objects from the same stimulus class were shown. The task of the subject was to indicate whether the target was present in the subsequent stimulus array. The number of targets shown in the first 500 ms duration was varied from 1 to 15 objects in steps of 2. The visual search rate was calculated and ranged from 11 ms/item (color) to 127 ms/item (cubes). The threshold number of objects stored in memory ranged from 1.6 (cubes) to 4.4 (colors). According to this study, if the objects tested were simple objects with little visual information, then the number of objects stored might be four or five, similar to the results of Luck et al. (1997). If the objects tested had more visual information or visual features, the storage capacity decreased.

1.4. “Leaky flask model” replacing Leaky hour glass model:

From the above literature, the major bottleneck in information processing was concluded to be in the visual short term memory. Based on this conclusion, a leaky hourglass analogy was proposed for information processing and storage capacity. According to this analogy, initial processing involves a series of parallel processing from retina to visual cortex. This parallel structure helps in processing a large amount of information in a quick time. The information is transferred to the first memory stage, sensory memory, which has a very large capacity to hold information, but the information decays quickly thereby resulting in a limited time span of storage. This limited time span of storage in the sensory memory is depicted as the “leaky” part in the leaky hour glass analogy. The next stage in information transfer is to visual short-term memory (VSTM), which has a limited capacity and a time span of storage of seconds. VSTM is considered to be the major bottleneck, i.e., the narrowest part of the hourglass, owing to its limited capacity. The bottom half of the hourglass represents long term memory, which is the final stage after the VSTM. Long term memory can accumulate a very large amount of information throughout one’s lifespan. In addition, the selection and the filtering functions of attention can play a significant role in visual information processing and can influence the capacity limits of all the memory components associated with the leaky hourglass analogy. (Fig-1-1)

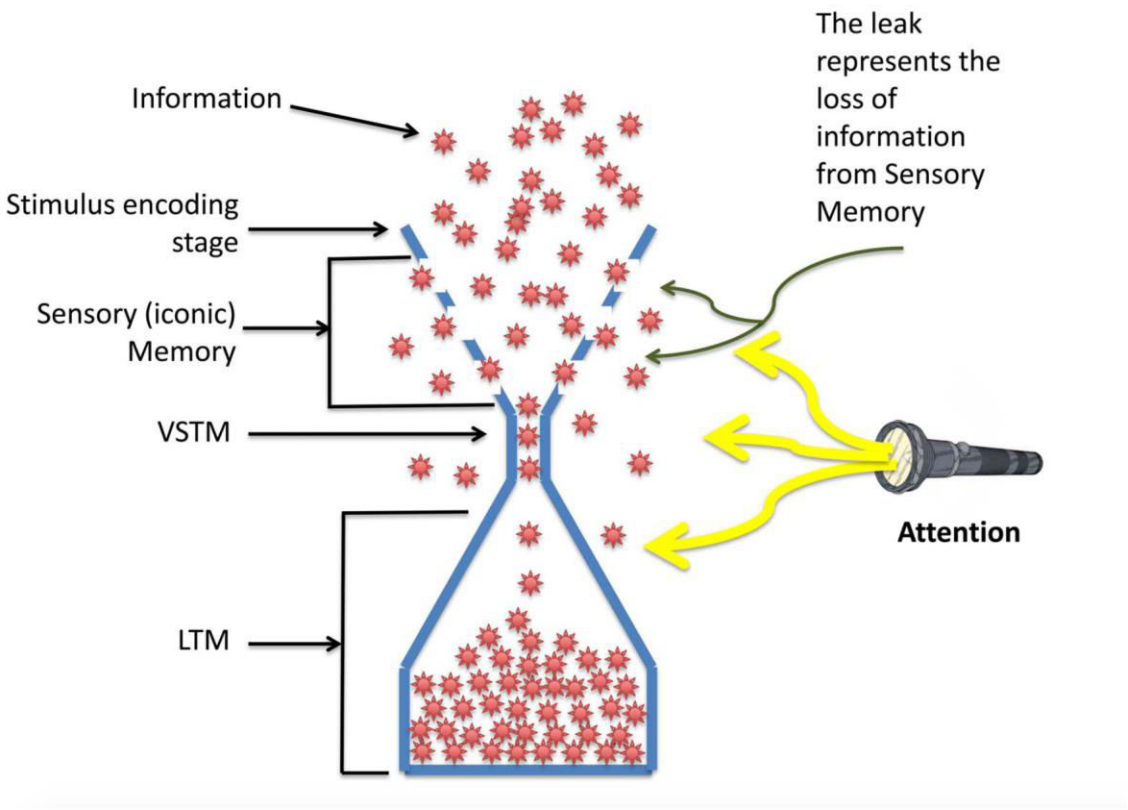

Figure 1- 1. Leaky hourglass analogy for information processing and storage.

Parallel processing from retina to visual cortex allows a large amount of information transfer. The information that is transferred goes through the sensory memory stage, which has a large capacity but a limited time span of storage. In the leaky hourglass analogy, the loss or the leak in the information in the sensory memory stage denotes the limited span of storage in sensory memory. The next stage is VSTM, visual short term memory, considered to be the bottleneck of the hourglass. VSTM has a limited capacity for information storage. The bottom of the hourglass represents long term memory, which has a large capacity and can retain information throughout one's lifespan. In addition, the selection and the filtering function of attention can influence the capacity of all three stages. (Adapted from Ogmen et al., 2013)

Ogmen et al. (2013) addressed the question of whether the major bottleneck involved in the visual information processing is VSTM. This study used a multiple-object tracking paradigm to assess observers' (N=4) performance in specifying the perceived direction of motion of a cued target for various distractor set sizes. In the first experiment, the authors probed the stimulus encoding stage; the cue was presented immediately after the stimulus motion termination. The results of this experiment indicate that performance dropped when there was an increase in the distractor set size. The drop in performance had a slope between 0.2% and 0.7% per distractor item. On the other hand, the performance dropped more quickly when there was an increase in target set size. This drop in performance had a slope between 2% and 2.5% per target item. This result indicates an important capacity limit at the early stage of stimulus encoding, which is prior to VSTM. In the second experiment, the authors used different cue delays to find out the information limit or bottleneck at different memory stages. The cue delays used were 0, 50, 100, 250, 500, 1000, and 3000 ms. The results of this experiment show that the distractor set-size was significant for the cue delays that were well within the sensory memory time span but was not significant for delays that accessed VSTM. Based on their results, the authors proposed a new leaky flask analogy instead of the leaky hourglass. The qualitative and the quantitative limits of the new analogy were estimated using various statistical models. The authors used a Gaussian+Uniform mixture model to replace the leaky hourglass analogy with two leaky flask models, one to describe the precision of information storage and the other to represent capacity.

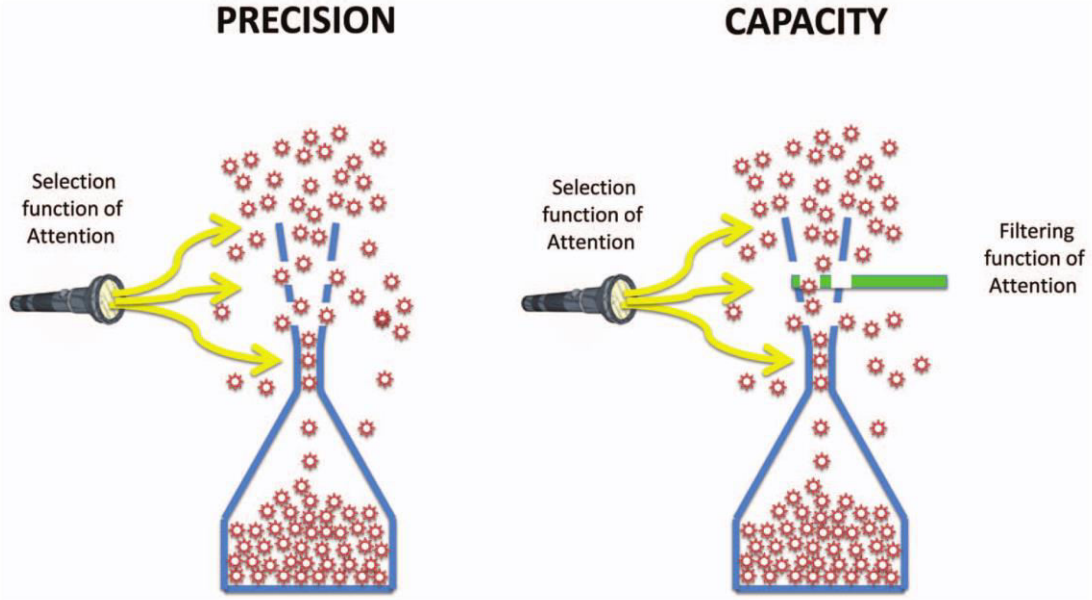

Figure 1- 2. Leaky flask model, Adpated from Ogmen et al., 2013.

The top portion of the leaky flask model is narrower to indicate that a capacity limit occurs prior to VSTM. The selection function of attention occurs all stages of memory, whereas the filtering function occurs only at the sensory memory stage (Refer to the green horizontal line in Figure 1-2).

This leaky flask model was determined to be applicable to different stimulus features like color, position, and the direction of motion. The principal bottleneck for all of these different features appeared to occur at the stimulus encoding stage, suggesting a significant loss of information in terms of quality and quantity before VSTM (Huynh et al., 2015).

1.5. Attention and Memory:

The influence of attention on visual working memory has been widely studied (Makovsik et al., 2007 & Fougnie et al., 2009). Persuh et al. (2012) studied the influence of attention on iconic memory. In this study, the authors also tested the two methods that are widely used to estimate iconic memory representations and the influence of attention on these representations. Iconic memory representation was estimated using a partial-report technique and cue-change detection technique. The role of attention was studied by using a visual search task with the memory task. Performance was estimated in the presence of an easy visual search task and hard visual search task. The performance dropped significantly when the attentional load was high suggesting that iconic memory transfer doesn't always occur in pre-attention stages.

Lapierre et al. (2013) explored the interaction between memory and attention during a multiple-object tracking paradigm. They also sought to understand if there is independent processing in the two visual hemifields when there is a relative dominance of attentional over memory processes, and vice versa. The results of this study indicate that attention

might be partially hemifield independent whereas memory is not, as there was substantial learning of trajectories and learning transfer from one hemifield to other.

Delvenne (2005) examined how the capacity limits of visual short-term memory change when colored targets are presented unilaterally in the left or right hemifield vs. bilaterally in the upper or lower vertical hemifields. The whole display screen was divided into four quadrants. Colored targets were split equally depending on the location condition, i.e. unilateral or bilateral. After 1000 ms, one colored target was displayed within one or two quadrants of the display for 200 ms. After a 1000-ms blank interval, colored squares were shown in a new set of locations. The task of the observers was to report whether the colored squares shown at the end of the trial were the same or different with respect to the colored targets shown at the start of the trial. The results of this experiment indicate that performance dropped when there was an increase in set size, both for unilateral and bilateral presentations. However, there was no significant difference in the performance between the unilateral and bilateral conditions for colored targets.

In the second experiment, the author wanted to assess hemifield independence for a task that involves only memory of spatial location. Instead of colored targets, the author used white targets. The results of this experiment reveal that the performance dropped as the set size was increased in both the unilateral and bilateral conditions, but was better in the bilateral condition than the unilateral condition. The author concluded that the later processing stages used for target identification and memory tasks has a contribution from both hemifields and may not show hemifield independence. On the other hand, a spatial location task that involves stimulus selection within the first stage of visual processing may show partially independent processing for each hemifield.

A subsequent study by Umemoto et al. (2010) showed a considerable bilateral advantage, as visual processing improved when the information was presented across both hemifields. The task of the observers was to adjust the orientation of the probed item to match the item that was shown at the start of the trial. According to the authors, a bilateral advantage was seen in later stages of working memory that involve the maintenance and storage of stimulus information. An electrophysiological study by Delvenne et al. (2011) indicated that retinotopic organization for identity tasks that involve colored targets exists in visual short term memory and there was a bilateral capacity limit of three or four targets. Many studies supported a substantial bilateral field advantage with respect to visual short term memory processing and also suggested independent attentional processing across the two hemispheres. (Delvenne, 2005; Delvenne et al., 2011; Delvenne and Holt, 2012; Holt and Delvenne, 2014 & 2015).

1.6. Attention and Visual Hemifields:

From a dorsal view, the cortex of the brain can be divided structurally into left and right hemispheres. These hemispheres are connected by the corpus callosum, a large network of fibers that plays a major role in transferring and communicating information from one hemisphere to other. Functionally, each hemisphere gets information primarily from the contralateral visual field. Information from both the visual fields is communicated between the two hemispheres by corpus callosum.

Luck et al. (1989) in their study of split-brain patients suggest that processing was faster when multiple stimuli were presented in a bilateral condition than a unilateral condition. These authors compared reaction times for visual search tasks for various set sizes in normal and in split-brain observers, when targets were presented either within the same

hemifield or across the two hemifields. In normal observers, the slope of the reaction time function for bilateral arrays was calculated to be 38.9 ms/item whereas the slope of the reaction time function for the unilateral arrays was calculated to be 42.6 ms/item. There was no significant difference between the slopes of reaction-time functions for the two types of arrays in normal subjects. On the other hand, in split-brain observers, the slope of the reaction-time function for bilateral arrays was found to be 25.3 compared to 47.3 ms/ item for unilateral arrays. This 50% drop in the slope for search in bilateral arrays in the split-brain observers indicates an advantage for independent hemifield processing. On comparing the percentage of correct responses, performance for the bilateral arrays was better than for the unilateral arrays in both split-brain and normal observers across the different set sizes.

Arguin and Colleagues (1990) tested whether there was a left vs. right visual field specialization for a task that involved visual search. The authors compared the reaction time for an attention task across two hemifields. They found no difference in reaction times for the left and right hemifields as a function of set size. This indirectly indicates that performance when the targets presented in the right hemifield is independent of the performance when the targets were presented in the left hemifield. This result might signify an allocation of independent attentional resources for each hemifield. The authors failed to record the performance when the targets were presented across the two hemifields.

Sereno and Kossyln (1991) did a series of attention experiments and compared the reaction times for targets within the same hemifield and across hemifields. In their study, they found that the reaction time was faster when the stimuli were presented across the hemifields than within the same hemifield. They also stated that there could be a hemifield-independent specific process in allocating attention that could either be facilitatory or inhibitory to each other. The results of this study were similar to those of Luck et al. (1989).

Alvarez and Cavanagh (2005) assessed whether the right and left hemifields have independent attentional resources or share attentional resources when attentional-tracking targets are presented within one hemi-field or across hemi-fields in normal observers. In their first experiment, the authors used two rotating sine wave gratings that were either shown in the same hemifield or were split across vertical hemifields. A probe was presented on one (one probe) or both gratings (two probes) at the start of the trial for 2 seconds. After 2 seconds, both gratings rotated for 3 seconds. During this time, the subject had to attentionally track the previous probe location on the rotating sine wave gratings while maintaining fixation on the fixation spot. A second probe was presented after 3 seconds on either one of the gratings; the task of the subject was to report the whether the probe presented at the end of the trial was of the same orientation as the probe presented at the start of the trial. The results of this experiment indicate that the performance was better when the gratings were presented across the two hemifields for both the one- and two-probe conditions. Performance dropped substantially more for two-

probe compared to one-probe gratings when the gratings were presented within a single rather than across the two hemifields.

Alvarez and Cavanagh (2005) did a similar experiment with a multiple object tracking paradigm. The authors presented two and four probe targets that were presented either in the same hemifield or across hemifields. The results were similar to the previous experiment, as the performance was better when the targets were presented across hemifields. Performance in the bilateral condition was similar whether 2 or 4 targets were probed. On the other hand, the percentage of correct responses dropped significantly when four compared to two probe targets were presented within the same hemifield. Alvarez and Cavanagh concluded that there could be independent attentional resources for attentional tracking within the left and right hemifields. They also stated that the maximum number of targets that could be tracked effectively was two in each hemifield.

Harasawa and Shioiri (2011) used stimuli and tasks similar to those in the Alvarez and Cavanagh (2005) study. The subjects' brain activity was recorded simultaneously using functional near-infrared spectroscopy during the tasks. Their results were similar to the Alvarez and Cavanagh (2005) study in that the performance of the subject was dependent on whether the locations the targets were in the same hemifield or across hemifields. Harasawa and Shioiri also found that an increase in attentional load, inferred from brain activity, occurred when there is an increase in the number of targets in the same visual hemifield. In addition, the increase in the attentional load was also dependent on how well the observers attended to that particular task.

In addition to the above-listed studies, many behavioral and imaging studies reported a bilateral hemifield advantage during the early stages of attentional processing and

reported hemispheric asymmetries that could be attributed to the attentional load in a particular hemifield (Proverbio et al., 1997; Macaluso and Frith, 2000; Awh and Pashler, 2000; Rhodes and Robertson, 2002; Kraft et al., 2005 & 2011; Alvarez et al., 2012; Störmer et al., 2014; Walter et al., 2016).

1.7. Significance:

To the best of our knowledge, no study has probed the contribution of one vs. two hemifields in the processing and storage of motion information, especially information about the direction of motion in sensory memory. In my study, I wish to study the hemifield contribution by presenting MOT stimuli within and across visual hemifields. The design and presentation of the stimulus was similar to those in a previous study by Huynh et al. (2015).

1.8. Specific Research Questions:

1. To investigate the processing of direction-of-motion information, its storage in sensory memory and VSTM, and the influence of independent attentional resources in one vs. two hemifields during these processes by presenting multiple object tracking stimuli with a cross-cuing approach at different cue delays for normal observers.
2. To appropriately modify the "leaky flask" model proposed by Ogmen et al. (2013) if there is any demonstrated hemifield independence in the processing and storage of motion information.

CHAPTER -2

2.1 Introduction:

Experiment I aimed to investigate the processing of direction-of-motion information, its storage during the stimulus-encoding stage, and the contribution of independent attentional resources in the two visual hemifields during this process by presenting multiple object-tracking stimuli with a cross-cuing approach at zero cue delay for normal observers.

2.2 Methods:

2.2.1.Apparatus:

A Visual Stimulus Generator system (Cambridge Research Systems, Cambridge, UK) with a VSG2/3 card driving a NANAO FlexScan color monitor was used to create and display stimuli. The programming was implemented in C++. The screen resolution was 800 x 600 pixels, of which 656 x 492 pixels (18.5 ° x 14 °, or 1.7 arcmin/pixel in terms of visual angle at 1 m) were used for object display. A central white fixation cross subtending 0.5° x 0.5° was used to control the observers' eye position. The screen was divided into four equal quadrants each subtending 8.75 ° x 5.5° by two thick black lines subtending a width of 3°, one passing vertically through the middle of the screen and the other horizontally. The observers were given a mouse to record their responses, and their heads were kept in position at a distance of 1.0 m in front of the monitor using a head and chin rest. The diameter of each dot object in the multiple-object tracking stimulus subtended a visual angle of 1°. Luminance of the dots was 100 cd/m^2. Dots were displayed on a gray background of luminance 40 cd/m^2.

2.2.2 Experiment:

This experiment was aimed at testing whether a hemifield independence exists in the processing of direction-of-motion information during the stimulus encoding stage. Observers started each trial by clicking a mouse. Objects of a specific set size (set sizes of 2, 4, 6, and 8 were used) that was either presented within the same hemifield or distributed across the two horizontal hemifields were used. All objects were white in color and remained stationary for 1 s, then started to move along linear trajectories at a constant speed of 3°/s for 200 ms, each in an independent, randomly selected motion direction. The motion directions were constrained so that no two objects had motion directions closer than 34°.

Initially, the objects were displayed within an imaginary circle of radius 5°. This was to make sure that the objects did not hit the edges of the display area and change direction while they were in motion. After 200 ms of motion, the objects disappeared. As this study aimed to probe processing during the stimulus-encoding stage, the cue delay was set to 0 s. Immediately after the objects stopped moving and disappeared, one object was cued by its position, and the task of the subject was to report its previous motion direction. Position was cued by a small black dot that was presented at the terminal position of the target object. The observers gave their responses using a mouse. Observers reported direction by moving the mouse cursor to indicate the target's direction of motion and confirmed their response by a mouse click. At the beginning of the experiment, the observers were informed that object position would serve as the cue for which object's direction of motion they should report. (See Figures 2-1 to 2-5).

The above procedure was repeated for different set sizes, either for objects presented across the two hemifields or within a single hemifield. Eye position was not monitored during the experiment. Hence, observers were constantly instructed during the experiment to keep their fixation on the fixation cross, in order to minimize eye movements and ensure that the targets were presented appropriately in either one or two hemifields. The experimental design for one cue-report combination was similar to that used in previous studies (Ogmen et al., 2013; Huynh et al., 2015). The experiment was carried out binocularly.

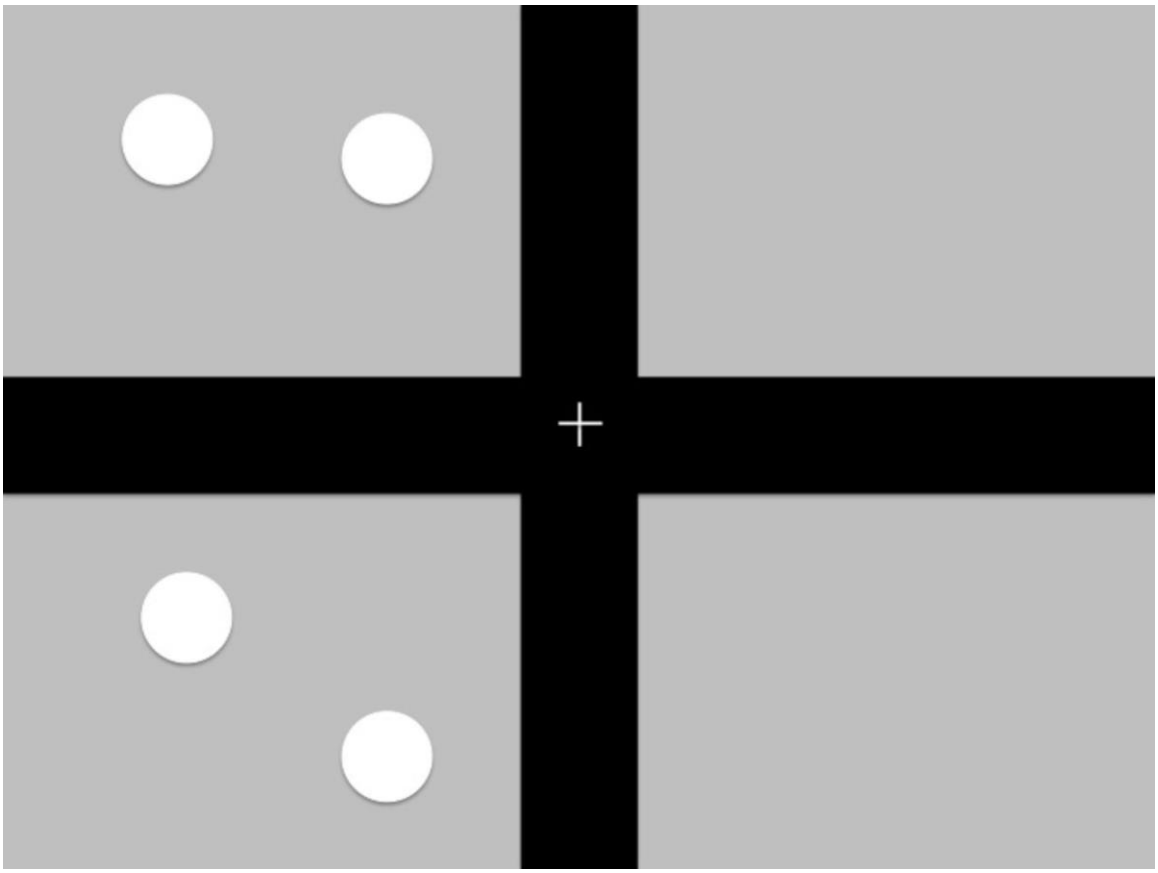

Figure 2-1. Unilateral condition – Targets in left hemifield

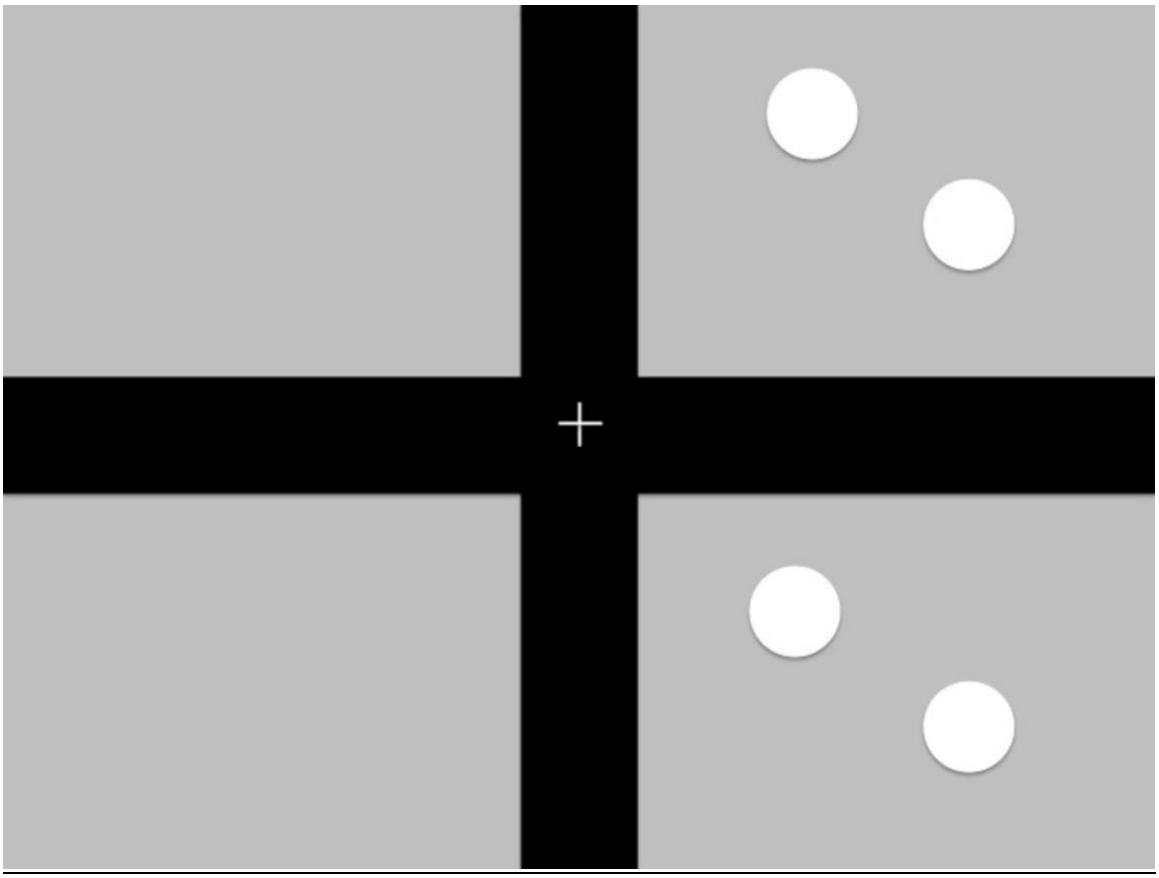

Figure 2-2. Unilateral condition – Targets in right hemifield

Figures 2-1 and 2-2. Example of the distribution of targets on trials in the unilateral condition. The objects were randomly distributed either in the left or the right hemifield.

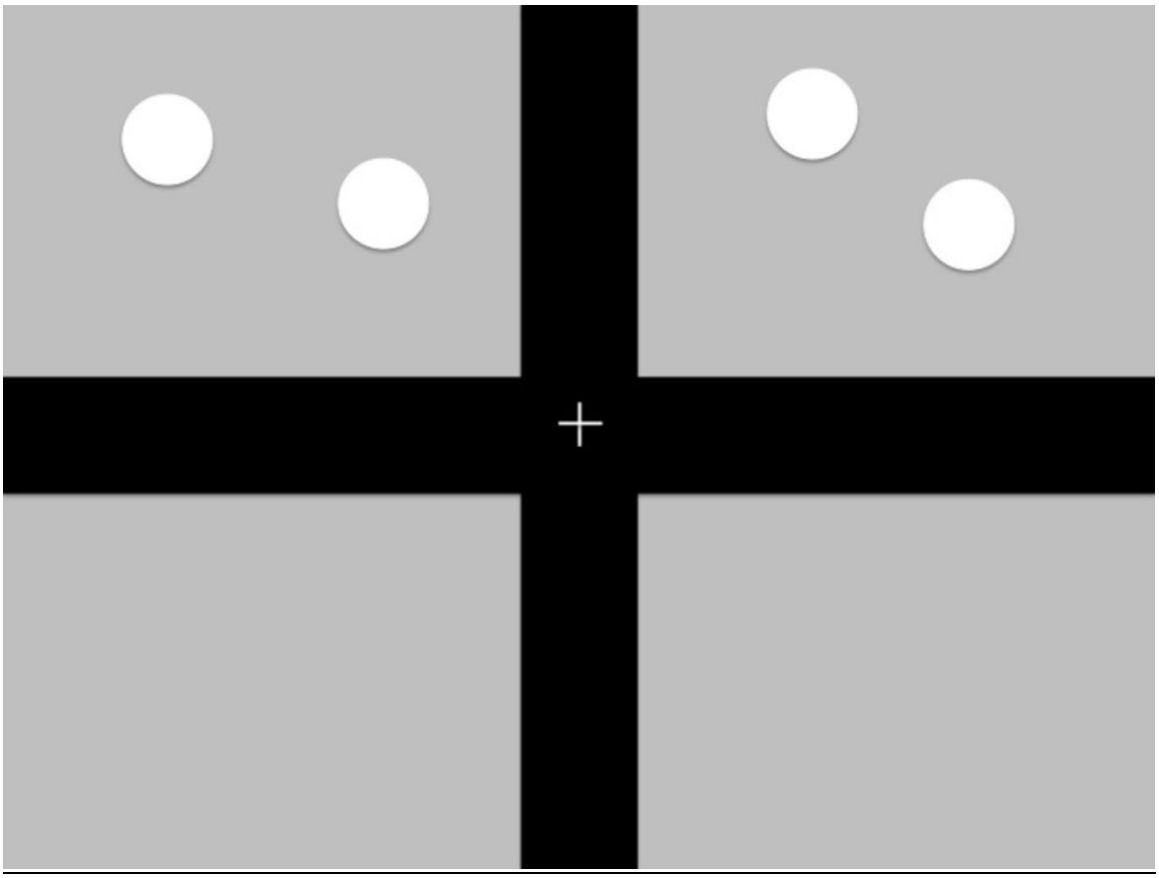

Figure 2-3. Bilateral condition – Targets in the upper vertical hemifield.

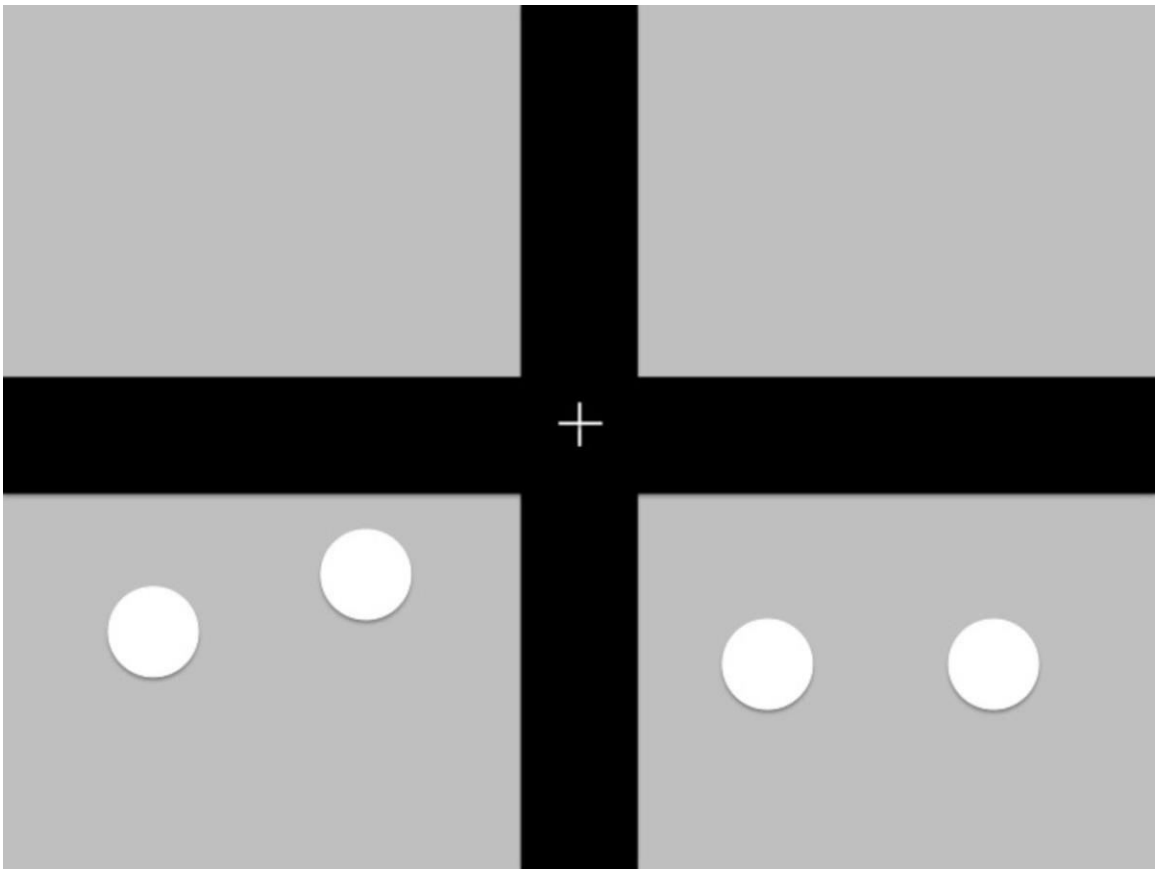

Figure 2-4. Bilateral condition – Targets in the lower vertical hemifield.

Figures 2-3 and 2-4. Example of the distribution of targets on a trial in the bilateral condition

The objects were randomly distributed either in the upper or the lower vertical hemifield.

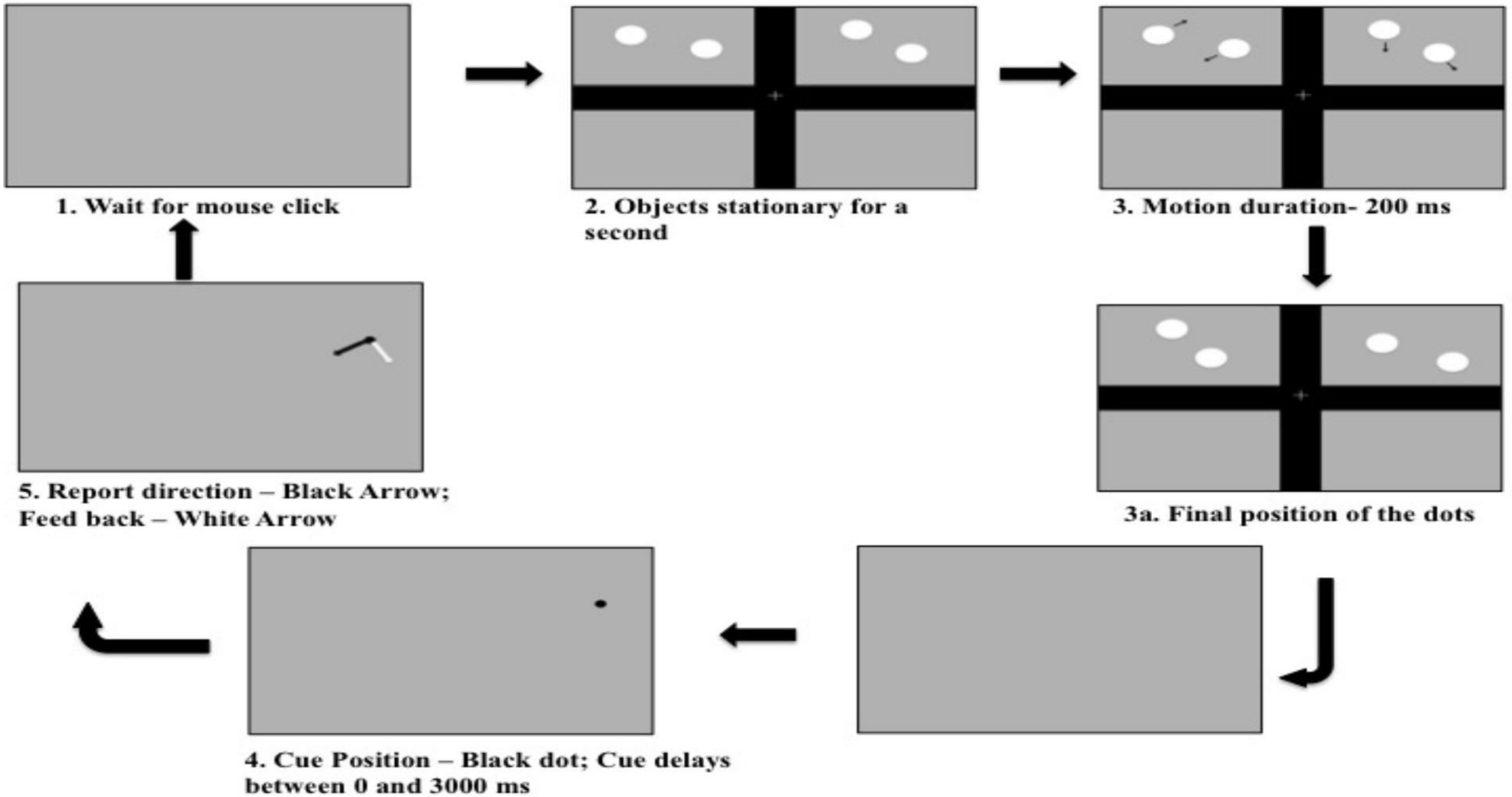

Figure 2-5. Time course of a trial for experiment 1, with no cue delay (to assess the stimulus encoding stage) and in experiment 2 with varying cue delays (to assess the sensory memory and short-term memory stages). In both experiments, the target's terminal position was cued by a black dot and observers reported the cued object's previous motion direction using a mouse to adjust the orientation of a black arrow.

2.2.3. Design:

At zero cue delay (Experiment 1), four set sizes (2, 4, 6, and 8) in two stimulus-location conditions (unilateral and bilateral) were tested. Three sessions of 20 trials for each stimulus combination were carried out. Three replications x 20 trials x 4 set sizes x 2 visual-field conditions x 1 cue delay = 480 trials per person. The order of set size and visual-field location were decided in a pseudo random manner.

2.2.4. Analysis:

The performance of the observers is reported as transformed performance, which is estimated from the magnitude of the error angle in specifying the cued target's direction of motion. The magnitude of the error angle is calculated as:

$|\varepsilon|$ = |the angle of true direction of motion - reported angle| (Equation 1)

Transformed performance (TP) = $1 - \frac{|\varepsilon|}{(180°)}$ (Equation 2)

If the calculated TP was 1, performance was perfect and if it was 0.5, then performance was at chance.

2.2.5. Predictions:

The performance of the observers was estimated by how well they could match the true direction of the motion. The error magnitude and the transformed performance (refer to Equations 1 and 2 above) was computed for different stimulus-location conditions, set sizes, and cue delays (experiment 2).

This chapter is aimed at investigating the hemifield advantage at the stimulus encoding stage. The mean the TP of the observers was expected to be influenced by two factors: set size and visual-field location. We analyzed the results using two-way repeated–measures ANOVA, with correction for sphericity if needed. The first null hypothesis was there should be no difference in the mean TP across the two different visual-field conditions. The second null hypothesis was there should be no difference in the mean TP across different set sizes.

A third null hypothesis was no interaction effect exists between the two factors of visual-field location and set size, or that these factors are independent. The general trend we expected was that performance should gradually decrease to chance level as the set size increased for all conditions, suggesting a capacity limit to visual processing that occurs at the stimulus-encoding stage. If there is no influence of visual-field location, we would expect the ANOVA to reveal a significant main effect of set size, no effect of visual-field location, and no interaction between the set size and the visual-field location. If there is a significant main effect of stimulus location, as one would predict from the bilateral advantage described in previous studies (Luck et al., 1981; Sereno and Kosylyn, 1991; Alvarez and Cavanagh, 2005), then the mean TP would be expected to be better in the bilateral than in the unilateral condition. In this case, ANOVA would give a main effect of stimulus location.

The existence of a bilateral advantage might be expected to result also in a significant interaction between the set size and the visual-field location. From the Figure 2-6, TP could be equal for both visual-field conditions for a small set size but drop less slowly in

the bilateral than the unilateral condition. This should result in a significant interaction. With respect to error magnitude, the error magnitude is expected to gradually increase with an increase in the set size. If a bilateral advantage exists, then the amount of the increase in the error magnitude would be expected to be less in the bilateral condition than the unilateral condition.

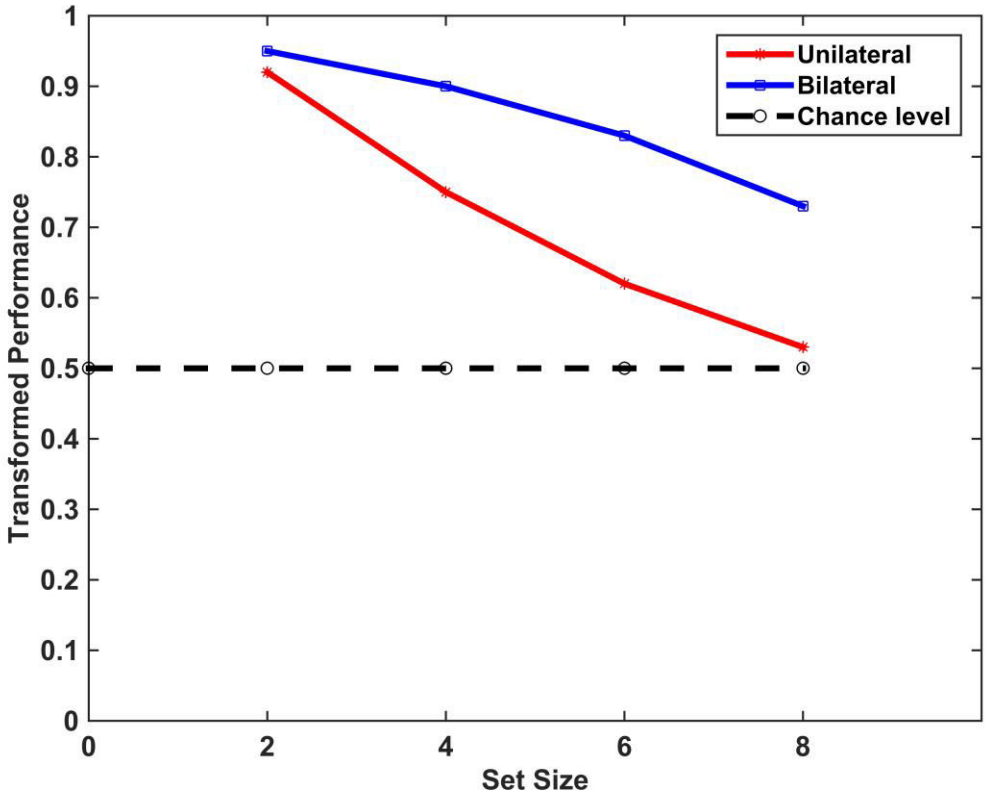

Figure 2-6. Predicted mean transformed performance as a function of set size for unilateral and bilateral hemifield stimulus locations for no cue delay.

We expected a significant difference between visual-field conditions for large but not small set sizes. We also expect a non-parallel drop in TP for the two conditions that creates the interaction. Blue – Predicted bilateral; Red- Predicted unilateral; Dashed – Chance level.

2.2.6. Participants:

Nine naïve observers as well as the author (26.2±2.5 years; Range: 24-30 years of age) with normal vision or corrected-to-normal vision were recruited for the study. Experiments were conducted according to a protocol adhering to the Declaration of Helsinki and approved by the University of Houston Committee for the Protection of Human Subjects.

2.2.7. Data Analysis:

The data of one subject were not consistent across blocks of trials and performance was near chance for most of the set sizes. The data of this subject were not included in the analysis. The data from the remaining nine observers were subjected to descriptive and inferential statistics using Microsoft Excel (2003) and STATA (StataCorp. 2015. *Stata Statistical Software: Release 14*. College Station, TX: StataCorp LP).

2.3. Results:

The transformed performance for all observers was determined for each set size and visual-field condition and the average transformed performance across all observers for each set size was then calculated and plotted. In Figure 2-7, the average transformed performance is plotted on the y-axis and the set size is plotted in the x-axis for the unilateral and bilateral stimulus conditions. A two-way repeated measures ANOVA showed a significant main effect of set size on performance: $F(3,56) = 218.99$, $p<0.0001$, $\eta_p^2 = 0.9215$. Specifically, average performance gradually decreased as a function of the set size. This decrease was consistent for both the unilateral and bilateral visual-field

conditions (see Table 2-1 and 2-2). Consistent with this observation, there was no main effect of visual-field condition on performance: $F(1,56) = 0.12$, $p=0.7285$. There also was no significant interaction between set size and location on the observers' performance: $F(3,56) = 1.21$, $p=0.3134$. As an additional analysis, we compared the performance of the observers when the targets were presented in either the upper or the lower half of both hemifields and found no difference: $F(1,56) = 1.15$, $p = 0.2879$. Taken together, the results indicate that the location of the targets, unilateral vs. bilateral or upper vs. lower visual field did not significantly influence the observers' performance. (Refer to Appendix A for each individual subject's performance.)

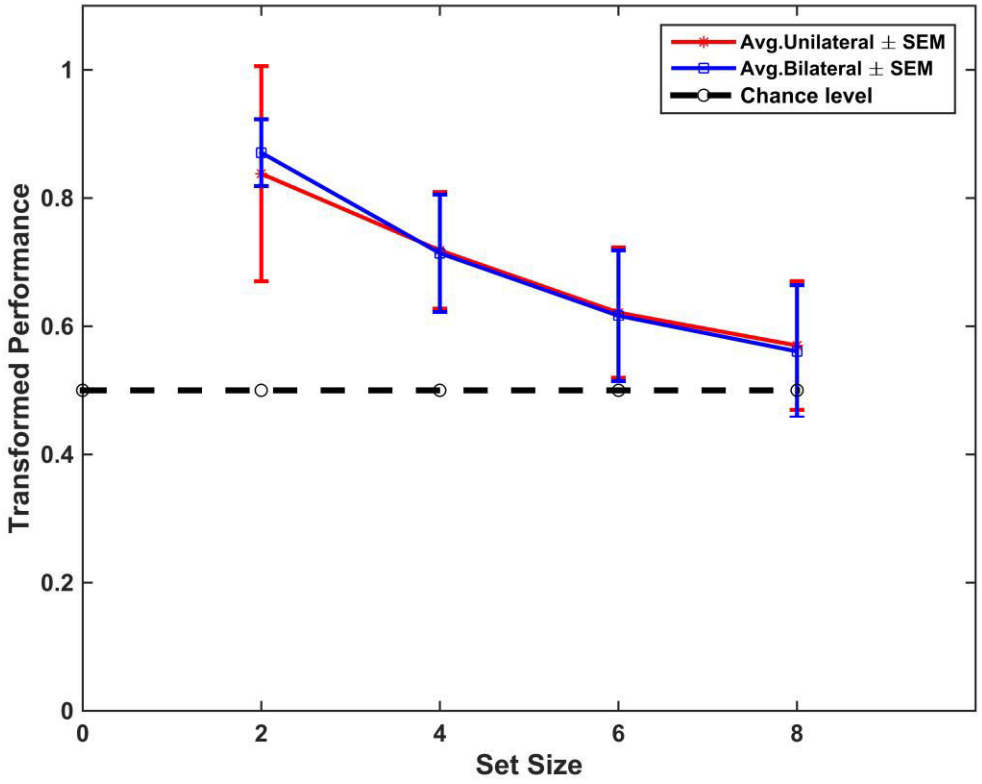

Figure 2-7. Mean TP of all observers (N=9) at zero cue delay as a function of set size.

The data plotted in red denote the unilateral condition and the data plotted in blue denote the bilateral condition. Chance performance is 0.5, which is indicated by a black dashed line. Error bars indicate ±1 Standard Error of the Mean (SEM).

Table 2-1. Average Transformed Performance across all observers for bilateral and unilateral visual-field conditions for various set size.

Set Size	Bilateral – Average Transformed Performance	Bilateral SEM	Unilateral – Average Transformed Performance	Unilateral - SEM
2	0.87	0.052	0.84	0.168
4	0.71	0.092	0.72	0.091
6	0.62	0.102	0.62	0.102
8	0.56	0.103	0.57	0.100

Table 2-2. Average transformed performance for each observer for the bilateral and unilateral visual-field conditions for various set size.

Subject	Set size	Bilateral Avg. TP	Bilateral SEM	Unilateral Avg.TP	Unilateral SEM
EAO	2	0.846	0.025	0.838	0.022
	4	0.729	0.031	0.720	0.013
	6	0.636	0.040	0.704	0.036
	8	0.623	0.041	0.654	0.039
FLX	2	0.857	0.022	0.881	0.016
	4	0.651	0.042	0.762	0.029
	6	0.606	0.040	0.582	0.044
	8	0.506	0.041	0.555	0.040
NGS	2	0.831	0.029	0.804	0.031
	4	0.718	0.034	0.675	0.039
	6	0.594	0.040	0.578	0.039
	8	0.578	0.038	0.577	0.041
AKS	2	0.898	0.010	0.900	0.017
	4	0.711	0.038	0.768	0.034
	6	0.684	0.038	0.676	0.036
	8	0.618	0.043	0.611	0.039
NGA	2	0.890	0.019	0.856	0.021
	4	0.768	0.036	0.756	0.028
	6	0.550	0.039	0.655	0.039
	8	0.521	0.038	0.573	0.040

Table 2-2, continued. Average transformed performance for each observer for the bilateral and unilateral visual-field conditions for various set size.

Subject	Set size	Bilateral Avg. TP	Bilateral SEM	Unilateral Avg.TP	Unilateral SEM
RAV	2	0.879	0.017	0.797	0.030
	4	0.688	0.035	0.696	0.037
	6	0.629	0.038	0.620	0.038
	8	0.545	0.040	0.468	0.036
MJK	2	0.873	0.022	0.882	0.016
	4	0.696	0.033	0.725	0.038
	6	0.579	0.044	0.586	0.039
	8	0.534	0.038	0.617	0.034
VIG	2	0.856	0.019	0.732	0.037
	4	0.715	0.038	0.732	0.038
	6	0.613	0.041	0.559	0.039
	8	0.549	0.039	0.536	0.038
SUY	2	0.907	0.009	0.866	0.020
	4	0.759	0.031	0.691	0.039
	6	0.657	0.034	0.631	0.042
	8	0.571	0.041	0.542	0.039

2.4. Discussion:

In this experiment, I wanted to investigate whether there was any improvement in the visual processing during the process of stimulus encoding stage when the targets were presented on both hemifields when compared to targets shown in the same hemifield. I calculated the subjects' performance in reporting the direction of motion of a cued object using a multiple-object tracking paradigm. Performance gradually dropped as a function of set size. Specifically, the performance for set size 2 was between 80 and 90% for all subjects where as the performance for set size 8 dropped considerably and was between 50 and 60% for all subjects. This drop in performance as a function of set size was seen in both the unilateral and bilateral visual-field conditions.

This drop in performance due to an increase in the number of items is consistent with previous studies (Luck et al., 1989; Ogmen et al., 2013; Huynh et al., 2015). Moreover, if we combine the performance of unilateral and bilateral conditions across set sizes, we get a transformed performance of 0.69. The average performance for the unilateral and bilateral conditions across set sizes was equal. A recent study by Huynh et al. (2015) reported a mean performance of 0.80 for the task where position was cued and direction of motion was reported. Huynh et al. (2015) reported position is an effective cue when direction of motion is reported. In our study, we found a drop of 10% in performance compared to Huynh et al. for a task where position was cued and direction of motion was reported.

This difference in performance could be due to a difference in the experimental set up. In contrast to the current study, Huynh et al. (2015) used differently colored targets. In

addition to the position cue that specified that target to report, the colors of the targets might have provided additional information that enhanced the observers' performance.

Our results are consistent with the finding reported in recent studies (Ogmen et al., 2013; Huynh et al., 2015) that the bottleneck of information processing occurs during the stimulus encoding stage and not in the VSTM.

We did not monitor the eye positions during the experiment but subjects were instructed to fixate continuously on the fixation cross that was provided. We assume that our results would be not be influenced substantially by spurious smooth-pursuit or saccadic eye movements as the duration of motion was short and the target motion was unpredictable.

2.5 Conclusion:

The findings of this experiment provide no evidence for a bilateral advantage at the early stimulus-encoding stage of visual information processing. There was a monotonic decline in performance from target set size = 2 to set size = 8, which suggests that a bottleneck of information processing occurs at this stimulus encoding stage, similar to the results of previous studies (Ogmen et al., 2013; Huynh et al., 2015).

CHAPTER -3

3.1. Introduction:

Experiment II aimed to investigate the processing of direction-of-motion information within and across the two hemifields in normal observers, as well as the storage of this information during the sensory-memory and visual short-term memory stages, by presenting multiple object-tracking stimuli with a cross-cuing approach at different cue delays.

3.2. Methods:

3.2.1.Apparatus:

The same experimental set up described in section 2.2.1 was used for this experiment.

3.2.2. Experiment:

This experiment was aimed at testing whether a hemifield independence exists in the processing and storage of motion information during the sensory memory stage and visual short-term memory stage (VSTM).

Two set sizes were chosen for the second experiment. One of them, small, was a set size of two, for which transformed performance in Experiment 1 was close to 0.9. A second, larger set size of 4 objects also was chosen as, based on the results of experiment 1, performance was expected to remain above chance for cue delays up to 3000 ms, despite the expected deterioration compared to zero cue-delay. In separate blocks of trials, targets with one of the two chosen set sizes were presented in two visual-field conditions (unilateral and bilateral) and with one of the following six cue delays: 50 ms, 100 ms, 250 ms, 500 ms, 1000 ms, and 3000 ms. In other words, unilateral and bilateral presentations

and set size varied pseudo-randomly from block to block, but cue delays were interleaved randomly.

Observers started each trial by clicking a mouse. Objects of a specific set size (set sizes of 2 = smaller and 4 = larger) were presented either within the same hemifield or split across the two horizontal hemifields. All objects were white in color and remained stationary for 1 s, then started to move along linear trajectories at a constant speed of 3°/s for 200 ms, each in an independent, randomly selected motion direction. The motion directions were constrained so that no two objects had motion directions closer than 34°.

Initially, the objects were displayed within an imaginary circle of radius 5°. This was to make sure that the objects did not hit the edges of the display area and change direction while they were in motion. After 200 ms of motion, the objects disappeared. As this study aimed to probe motion information processing during sensory memory and VSTM, cue delays of 50, 100, 250, 500, 1000, and 3000 ms were used. Immediately after the objects stopped moving and disappeared, one object was cued by position, and the task of the subject was to report its previous motion direction. Position was cued by a small black dot that was presented at the terminal position of the target object. The observers gave their responses using a mouse. Observers reported direction of motion by moving the mouse cursor to set the orientation of a black arrow (see Figure 2.5) and confirmed each response with a mouse click. At the beginning of the experiment, the observers were informed that object position would serve as the cue about which object's direction of motion they should report.

This procedure was repeated for the two different target set sizes, presented both within the same hemifield and distributed across hemifields. Observers were instructed to look steadily at a fixation cross during the experiment to minimize eye movements. The experiment was carried out binocularly. In the study by Ogmen et al. (2013), the dots were displayed at their terminal spatial location during the cue delay, whereas the dots disappeared during the cue delay in the study by Huynh et al. (2015). The latter procedure was followed in my study. The reason for choosing this protocol was to avoid any a priori attentional focus on any of the items or locations, which might influence the observers' performance. In addition, the studies by Ogmen et al (2013) and Huynh et al (2015) showed no significant difference for an object set size of five between the averaged performance with and without persistence of the stationary target objects during the cue-delay period.

3.2.3. Design:

Three replications X 20 trials X 2 set sizes X 2 visual-field conditions X 6 cue delays = 1440 trials per observer. The combinations of set size, cue delay, and visual-field location were presented in a pseudo random order. The duration for each block of 20 trials was less than 15 min. Observers were given adequate breaks in between successive blocks.

3.2.4. Analysis:

The performance of the observers is reported as transformed performance, which is estimated from the magnitude of the error angle in specifying the cued target's direction of motion. The magnitude of the error angle is calculated as:

$|\varepsilon|$ = |the angle of true direction of motion - reported angle| (Equation 1)

Transformed performance (TP) = $1 - \frac{|\varepsilon|}{(180°)}$ (Equation 2)

If the calculated TP was 1, the performance was perfect and if TP was 0.5, then performance was at chance.

3.2.5. Predictions:

The mean TP of the observers for the set of 6 cue delays was expected to be influenced by set size (N = 2 and 4 in this experiment) and by the different visual-field conditions. We ran a three-way repeated-measures ANOVA, with correction for sphericity if necessary. The factors that were included in the ANOVA were set size, visual-field location, and cue delay. The null hypothesis was the mean TP across different set sizes, visual-field locations, and cue delays would have no difference. A second null hypothesis was that the three factors of set size, visual-field location, and cue delay are independent of each other, as indicated by no significant two-way or three-way interactions between set size, visual-field condition and cue-delay in the ANOVA.

If there was no influence of the visual-field condition, we expected to find a main effect of set size with no interaction between the visual-field condition and set size or cue delay. However, if a bilateral advantage exists, then the mean TP for the bilateral visual-field

condition should be significantly better than for the unilateral visual-field condition (Figures 3-1 and 3-2). In addition, we expected to find a gradual decrease in performance with an increase in the cue delay. This drop in performance should be minimal in the bilateral condition if there is any bilateral advantage (Delvenne, 2005; Delvenne et al., 2011; Delvenne and Holt, 2012). Hence, if the visual-field location has a significant main effect, then we also expected a significant interaction between the set size and the visual-field condition. We also anticipated that the within-subject's main effect in the ANOVA due to visual-field location might vary with cue delay and that we might see significant interactions.

It has been shown in many studies that by 3 s, VSTM comes into play, which suggests that the duration of sensory memory is shorter than three s. I decided to average the data of all observers and group the results into just two memory categories: sensory memory and VSTM. In other words, transformed performance for different cue-delays that are attributed to the same memory system were combined. Based on the previous studies, sensory memory is shorter than 3s (Sperling, 1960; Shooner et al., 2010). The decay of sensory memory tends to show an exponential trend and another way to delineate sensory memory from VSTM is to fit an exponential function to the results at the different cue delays. It is assumed that the steady-state level of exponential decay indicates the operation of VSTM (Ogmen et al., 2013) and that the time prior to the steady-level of exponential decay includes the duration of sensory memory. In my study, I did not do an exponential fit to the data for each subject; rather I chose the time limit of 1 second as the demarcation between sensory memory and VSTM (Ogmen et al., 2013; Huynh et al.,

2015). As the two longest cue delays that I used were 1s and 3s, any shift in the transition from sensory memory to VSTM within this interval would not affect my analyses.

This analysis by memory categories was done separately for each set size. I ran ANOVA to study the main effect of stimulus location, set size, and to look for significant interaction between the set size and the stimulus location. The null hypothesis was that no significant interaction between set size and visual-field condition will occur either for the durations categorized as sensory memory or as VSTM.

I expected a significant difference between the visual-field conditions for large but not small set sizes. The existence of a bilateral advantage might be expected to result also in a significant interaction between the set size and the visual-field location. From Figures 3-3 and 3-4, TP could be equal for both visual-field conditions for the smaller set size but slightly better in the bilateral than the unilateral condition. This should result in a significant interaction. This significant interaction was expected to be seen in both the sensory memory stage and the VSTM stage. On the other hand, I expected a large difference between the TPs in the bilateral and the unilateral conditions for the larger set size, suggesting a bilateral advantage with a significant interaction.

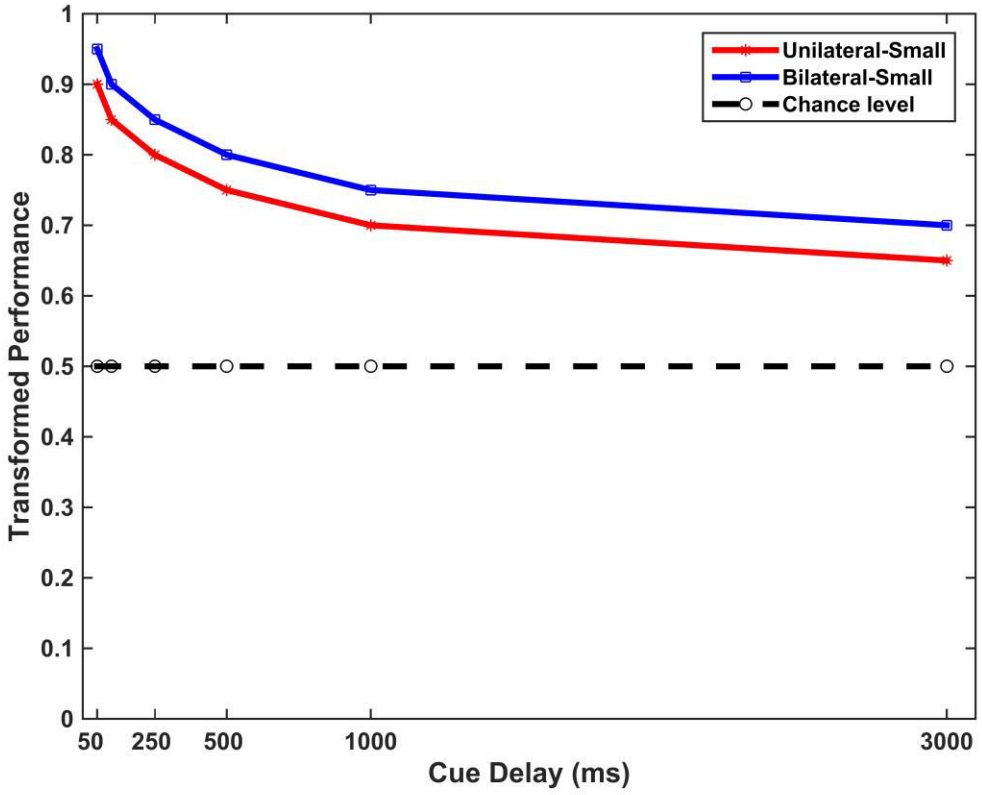

Figure 3-1. Predicted performance at different cue delays for the smaller set size for both visual-field conditions. Bilateral = Blue; Unilateral = Red; Chance = Black dashed line.

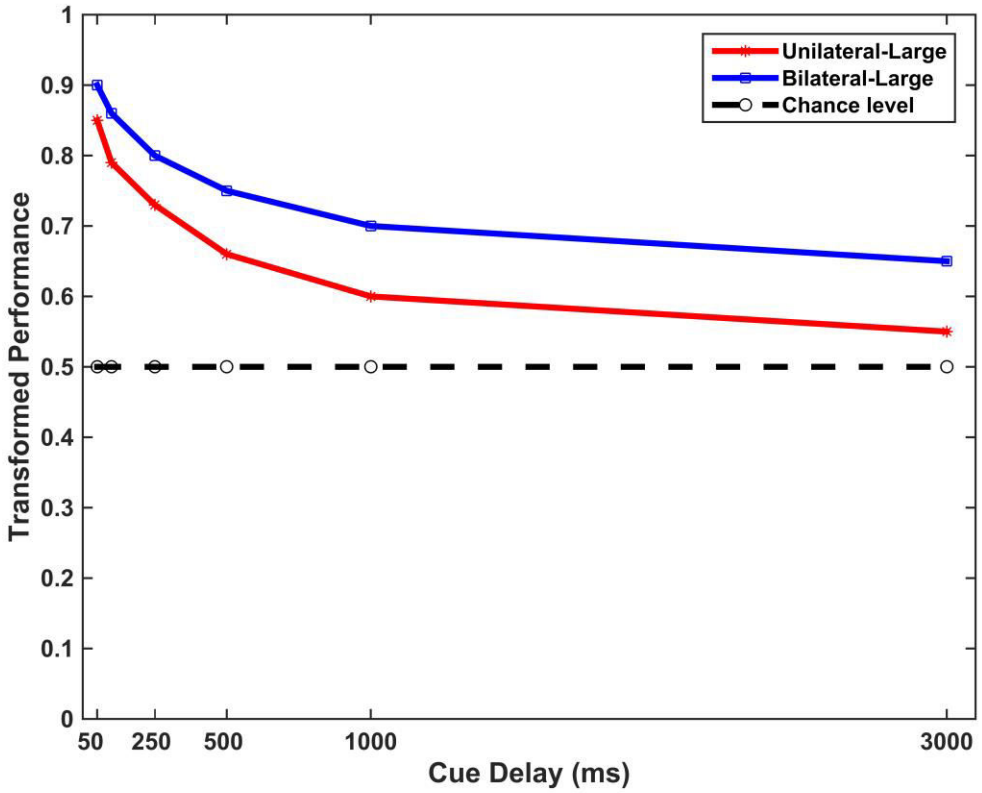

Figure 3-2. Predicted performance at different cue delays for the larger set size for both visual-field conditions. Bilateral = Blue; Unilateral = Red; Chance = Black dashed line.

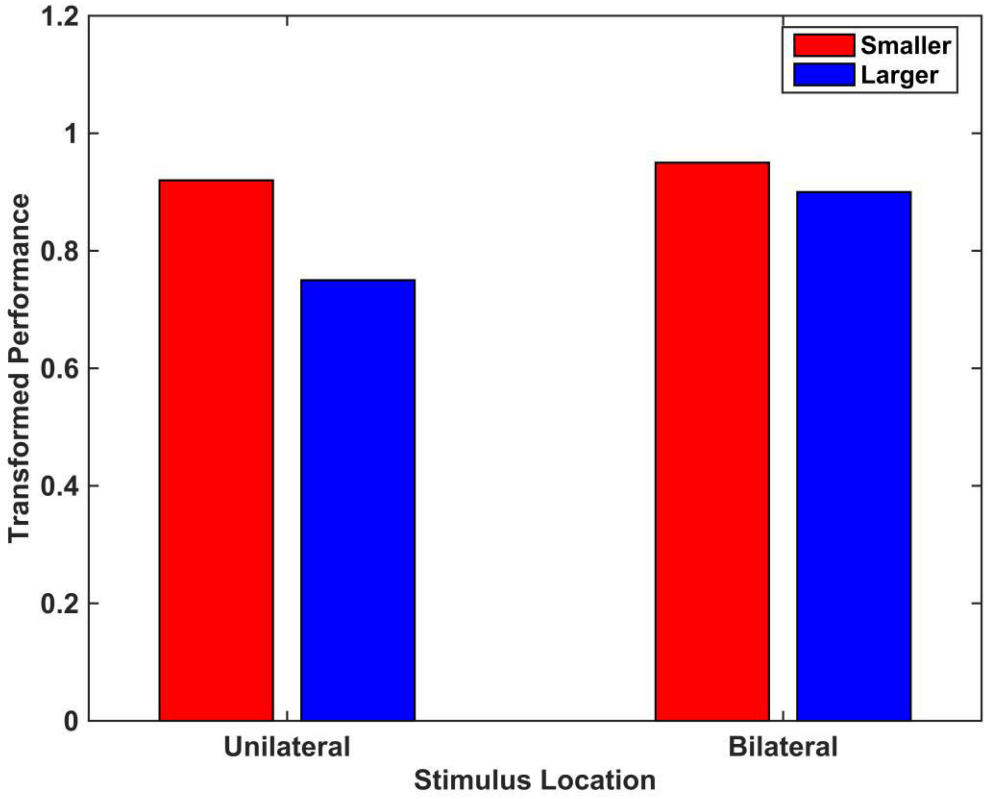

Figure 3-3. Predicted performance for the smaller and larger set sizes in the two visual-field conditions for cue delays corresponding to sensory memory.

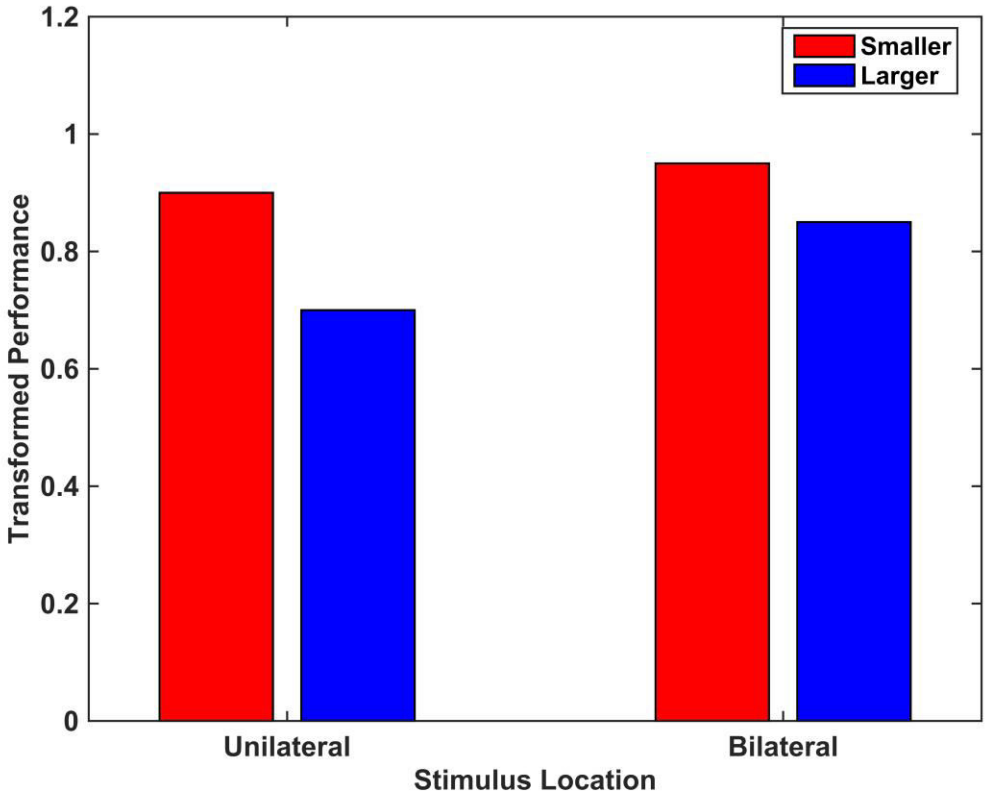

Figure 3-4. Predicted performance for the smaller and larger set sizes in two visual-field conditions for cue delays corresponding to the VSTM stage.

3.2.6. Participants:

Eight observers (25.8±2.3 years; Range: 24-30 years of age) with normal vision or corrected to normal vision, all of whom participated in the first experiment, were enrolled in this experiment. Experiments were conducted according to a protocol adhering to the Declaration of Helsinki and approved by the University of Houston Committee for the Protection of Human Subjects. Based on the subjects' performance in experiment 1, the smaller set size was set to 2 and larger set size was set to 4.

3.2.7. Data Analysis:

Data from eight observers were subjected to descriptive and inferential statistics using Microsoft Excel (2003) and STATA (StataCorp. 2015. *Stata Statistical Software: Release 14*. College Station, TX: StataCorp LP.)

3.3. Results:

The transformed performance for all observers was calculated for the smaller and larger set sizes and for different cue delays and the average transformed performance across all observers for each set size was then calculated (Tables 3-1 and 3-2) and plotted as a function of the cue delay. In Figure 3-5, the average transformed performance was plotted on the y-axis and the cue delay was plotted on the x- axis, separately for the unilateral and bilateral conditions. A three-way repeated measures ANOVA showed a main effect of set size on performance ($F(1,161) = 900.97$, $p<0.0001$, $\eta_p^2 = 0.8484$) and a small but significant main effect of visual-field location ($F(1,161) = 23.82$, $p<0.0001$, $\eta_p^2 = 0.1289$). Although average performance decreased slightly as a function of cue delay in

both the unilateral and bilateral visual-field conditions, the ANOVA indicated no significant main effect of cue delay $F(5,161) = 1.69$, $p=0.1408$. There also was no significant 3-way interaction between set size, cue delay, and visual-field condition ($F(5,161) = 0.82$, $p=0.6607$). There also were no significant 2-way interactions between set size and cue delay ($F(5,161) = 0.14$, $p=0.9817$), cue delay and location ($F(5,161) = 1.12$, $p=0.3535$), or set size and location ($F(1,161) = 1.76$, $p=0.187$). (Refer to Appendix B for individual subject plots).

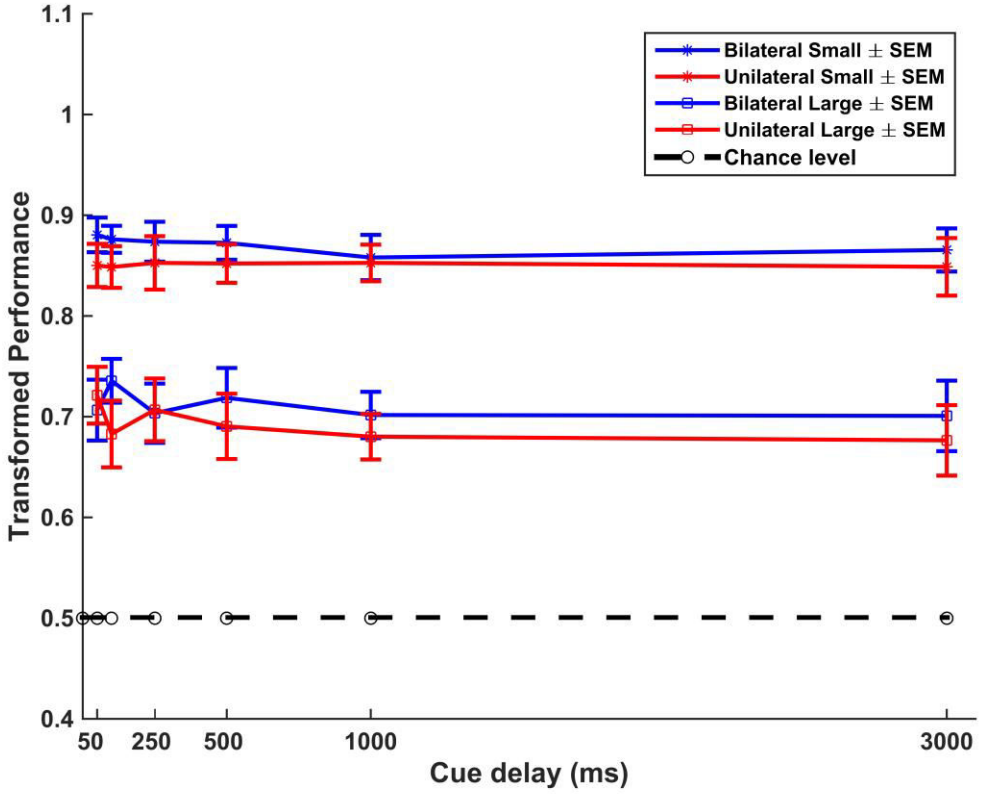

Figure 3-5. Average performance for smaller and larger set sizes in two visual-field conditions for different cue delays. Bilateral – Blue ; Unilateral – Red; Error bars: ±1 SEM.

Table 3-1. Performance for set size = 2 in the unilateral and bilateral visual-field conditions

Cue delay (ms)	Bilateral TP Smaller	Bilateral TP Smaller SEMs	Unilateral TP Smaller	Unilateral TP Smaller SEMs
50	0.880	0.017	0.850	0.021
100	0.876	0.013	0.849	0.021
250	0.873	0.020	0.853	0.026
500	0.873	0.017	0.852	0.019
1000	0.858	0.023	0.853	0.018
3000	0.865	0.021	0.848	0.029

Table 3-2. Performance for set size = 4 in the unilateral and bilateral visual-field conditions

Cue delay (ms)	Bilateral TP Larger	Bilateral TP Larger SEMs	Unilateral TP Larger	Unilateral TP Larger SEMs
50	0.701	0.030	0.721	0.028
100	0.736	0.021	0.683	0.033
250	0.703	0.029	0.707	0.031
500	0.719	0.030	0.690	0.032
1000	0.701	0.023	0.680	0.022
3000	0.70	0.035	0.676	0.035

I also grouped the data for different cue delays and averaged the performance. The performance at cue delays of 1000 ms and below were averaged and taken to represent performance at the sensory memory stage. The average performance at a cue delay of 3000 ms was considered to indicate performance at the stage of visual short-term memory (refer to Figures 3-6 and 3-7 and Tables 3-3 and 3-4).

Table 3- 3. Averaged performance for the set sizes = 2 and 4 in the unilateral and bilateral visual-field conditions for cue delays of 50 – 1000 ms (Sensory Memory stage).

GROUPED DATA - SENSORY MEMORY

Set Size	Bilateral TP Mean	Bilateral TP SEM	Unilateral TP Mean	Unilateral TP SEM
Small = 2	0.872	0.018	0.842	0.021
Large = 4	0.713	0.027	0.696	0.030

Table 3-4. Averaged performance for the set sizes = 2 and 4 in the unilateral and bilateral visual-field conditions for cue delays = 3000 ms (VSTM stage).

GROUPED DATA – VISUAL SHORT-TERM MEMORY

Set Size	Bilateral TP Mean	Bilateral TP SEM	Unilateral TP Mean	Unilateral TP SEM
Small = 2	0.866	0.021	0.828	0.029
Large = 4	0.700	0.035	0.677	0.035

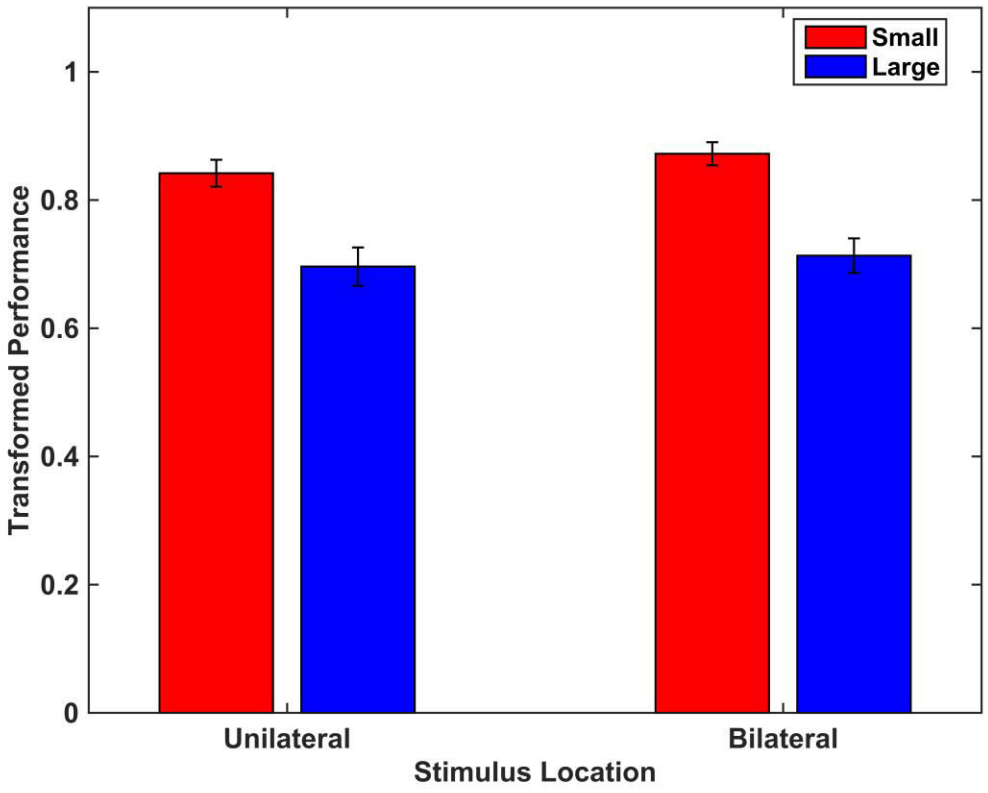

Figure 3- 6. Average performance at the sensory memory stage for smaller and larger set sizes for the bilateral and unilateral visual-field locations. Error bars: ±SEM. Smaller = Red; Larger = Blue.

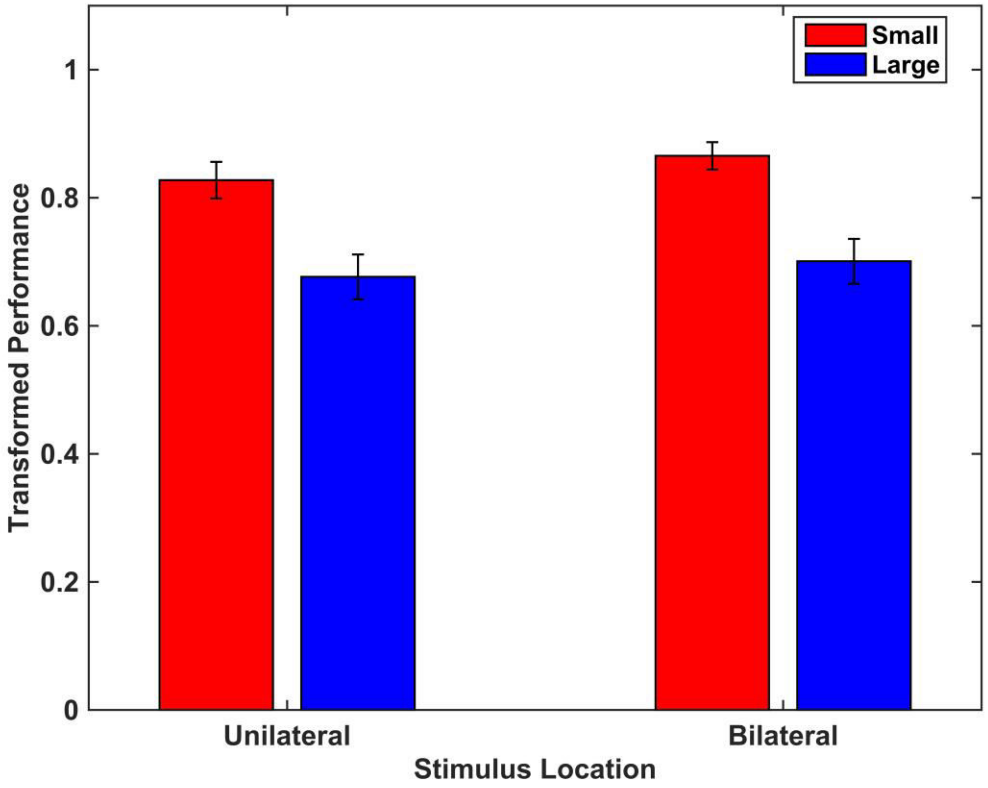

Figure 3-7. Average performance at the VSTM stage for smaller and larger set sizes for the bilateral and unilateral visual-field locations. Error bars: ±SEM. Smaller = Red; Larger = Blue.

From the grouped data (Figures 3-6 and 3-7 and Tables 3-3 and 3-4), the performance in the bilateral condition was 3-5% better than in the unilateral condition, both in the sensory-memory and VSTM stages. The grouped data also show a 15-20% decrease in performance as the set size increased from 2 to 4. This decrease was seen in both the unilateral and bilateral conditions and in both the sensory-memory and VSTM stages.

Two-way ANOVA run on these data confirms a main effect of visual-field location at the sensory memory stage ($F(1,21) = 367.86$, $p = 0.0071$) and a main effect of set size ($F(1,21) = 367.86$, $p<0.0001$). However, there was no significant interaction between set size and visual-field location at this stage ($F(1,21) = 0.72$, $p = 0.4047$).

On the other hand, there was no significant effect of visual-field location at the VSTM stage ($F(1,21) = 3.88$, $p = 0.062$) but there was main effect of set size on performance at the VSTM stage ($F(1,21) =101.22$, $p<0.0001$). There was no significant interaction between set size and location at the VSTM stage ($F(1,21) = 0.17$, $p = 0.6802$).

This small but significant effect of visual-field condition for the delays corresponding to sensory memory, but not for the 3-s delay corresponding to VSTM may reflect greater statistical power for the first comparison, based on pooling the results from 5 different cue delays.

3.4. Discussion:

In this experiment, I wanted to investigate whether there was any improvement in visual processing of direction of motion during sensory memory and/or VSTM stage when the targets were presented in both hemifields when compared to targets shown in the same hemifield. I calculated the subjects' performance in reporting the direction of motion of a cued object using a multiple-object tracking paradigm. From the statistical analysis, I infer that the visual-field location and set size influenced the performance in both the unilateral and bilateral conditions. The results indicate that performance was slightly enhanced by the presentation of the targets in both hemifields, suggesting a minimal bilateral advantage. The presence of this bilateral advantage is consistent with previous findings (Delvenne, 2005; Delvenne et al., 2011).

A surprising outcome of this experiment is the absence of a significant effect on performance of the cue delay. This result differs from the position cue – direction report condition of Huynh et al. (2015), in which performance for a target set size of 6 decreased monotonically as the cue delay increased. It is possible is that performance remained essentially unchanged for cue delays between 50 to 3000 ms in my experiment because direction-of-motion information for target set sizes of 2 and 4 could be transferred from sensory memory to VSTM. In agreement with this possibility, I replicated in one subject the drop-off in performance reported by Huynh et al. for a target set size of 6. As noted above in section 2.4, the performance of this subject was slightly worse at all cue delays in both the bilateral and unilateral conditions than that reported by Huynh et al. for set-size = 6, perhaps because the targets in my experiments did not include additional color information.

The results after grouping data from the 6 cue delays into sensory and VSTM stages indicate that a bilateral advantage was missing in the VSTM stage but not in the sensory-memory stage. The main effect after grouping the data was due to set size and not due to visual-field location. This is in contrast to the previous findings where a bilateral advantage was reported at the VSTM stage (Delvenne, 2005; Delvenne et al., 2011; Delvenne and Holt, 2012; Holt and Delvenne, 2014 & 2015).

On the other hand, a few studies (Oksama et al., 2008; Hudson et al., 2012) reported that a bilateral advantage might or might not occur, depending on the task. Considering the results of the first and the second experiments together, a robust bilateral advantage was not seen using my experimental set up. To confirm these results, I attempted to replicate the Alvarez and Cavanagh (2005) study with my experimental set up.

3.5 Conclusion:

The results of Experiment II suggest that the performance of subjects was influenced primarily by the number of items for used for tracking and not by the location of items in the visual-field. The result that set size influences the performance is consistent with the existing literature (Luck et al,. 1989 & 1997; Shooner et al., 2010; Ogmen et al., 2013; Huynh et al., 2015). From my results, one cannot ignore that a small bilateral advantage exists in the sensory memory stage processing but not in the VSTM stage. The evidence for a lack of a robust bilateral advantage in my study seems to contradict previous work (Alvarez and Cavanagh., 2005; Delvenne 2005; Delvenne et al., 2011; Delvenne and Holt, 2012; Holt and Delvenne, 2014 & 2015). Based on my results, I wish to postulate that a bilateral advantage for information processing is minimal across memory stages.

CHAPTER -4

4.1. Introduction:

The hemispheric advantage reported in previous studies was either absent or minimal in my study. Hence, I wished to replicate the multiple-object tracking experiment, using stimuli similar to the stimuli in my previous experiments but with a procedure and task (object identity vs. motion direction) as similar as possible to the Alvarez and Cavanagh (2005) study. Experiment III aimed to investigate the contribution of the two hemifields in a multiple-object-tracking paradigm by presenting multiple-object-tracking stimuli to normal observers.

4.2. Methods:

4.2.1.Apparatus:

The same experimental set up described in section 2.2.1 was used for this experiment.

4.2.2. Experiment:

This experiment aimed to test whether there is any hemifield independence in a multiple–object-tracking paradigm, using my experimental setup. I wished to replicate the findings of Alvarez and Cavanagh (2005) with my set up.

Observers started each trial by clicking a mouse. Two or four target objects, randomly chosen from trial to trial from a total of ten objects, were black. The rest of the "distractor" objects were white. Objects were either presented within the same hemifield or split across the two horizontal hemifields. All objects remained stationary for 1 s, then started to move along linear trajectories at a constant speed of 3°/s, each in an independent, randomly selected motion direction for 200 ms. The motion directions were constrained so that no two objects had motion directions closer than 34°.

During the 200-ms motion period, all objects were white in color. Initially, the objects were displayed within an imaginary circle of radius 5°. This was to make sure that the objects did not hit the edges of the display area and change direction while they were in motion. After 200 ms of motion, all of the objects disappeared.

After the objects disappeared, one of the 10 objects was cued by presenting a small black dot at the object's terminal position, and the task of the subject was to report whether the cued object was one of the designated black targets at the start of the trial. The observers gave a yes or no response using a mouse: "yes" was indicated by a left click of the mouse and "no" was indicated by a right click of the mouse. After each trial auditory feedback was given; a short beep for a correct response and a long beep for an incorrect response.

At the beginning of the experiment, the observers were informed that position would serve as the cue about which object they should report and that their response should indicate whether the cued object was a (black) target or a (white) distractor. This procedure was repeated for two black targets and four black targets, presented either across the two horizontal hemifields or within the same hemifield (see Figures 4-1 to 4-9). Observers were instructed to look steadily at a fixation cross during the experiment, to minimize eye movements and ensure correct positioning of the moving objects in the visual field.

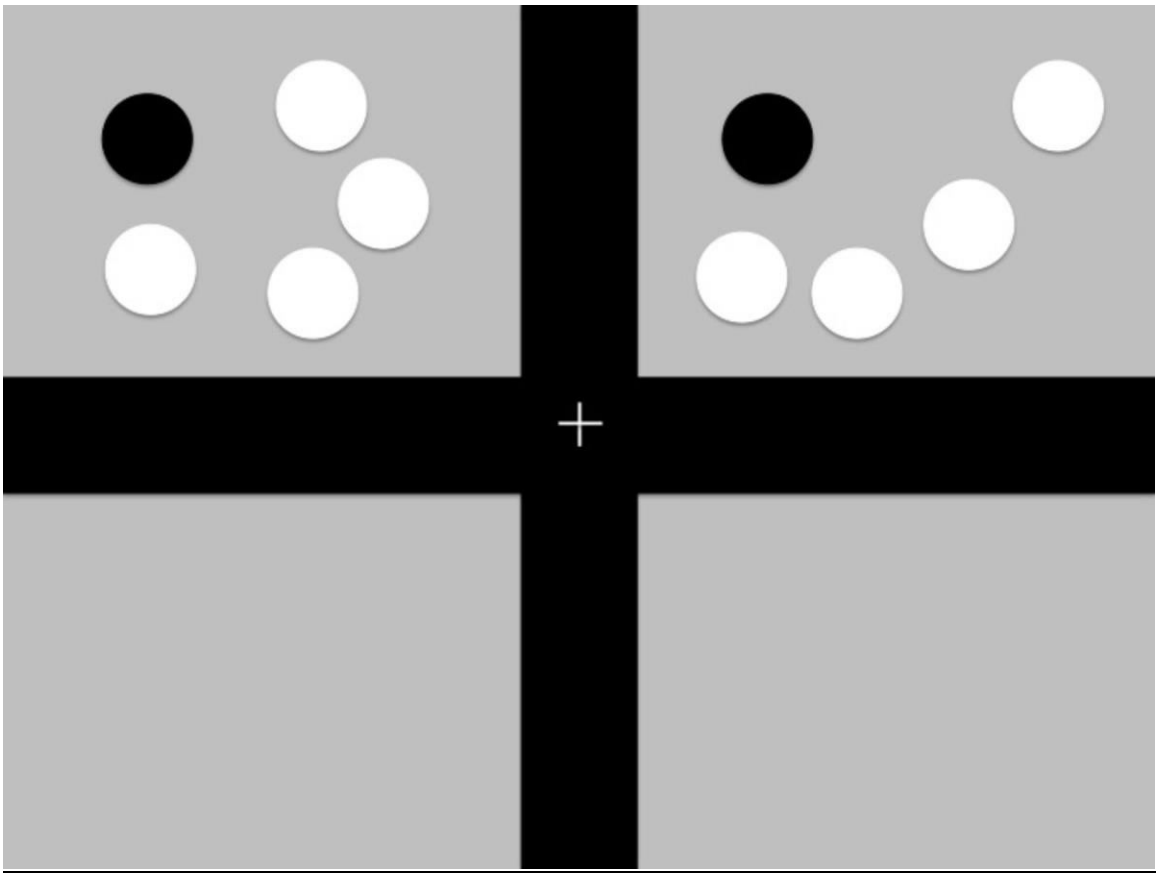

Figure 4-1. **Bilateral condition – Two-target condition in the upper vertical hemifield.**

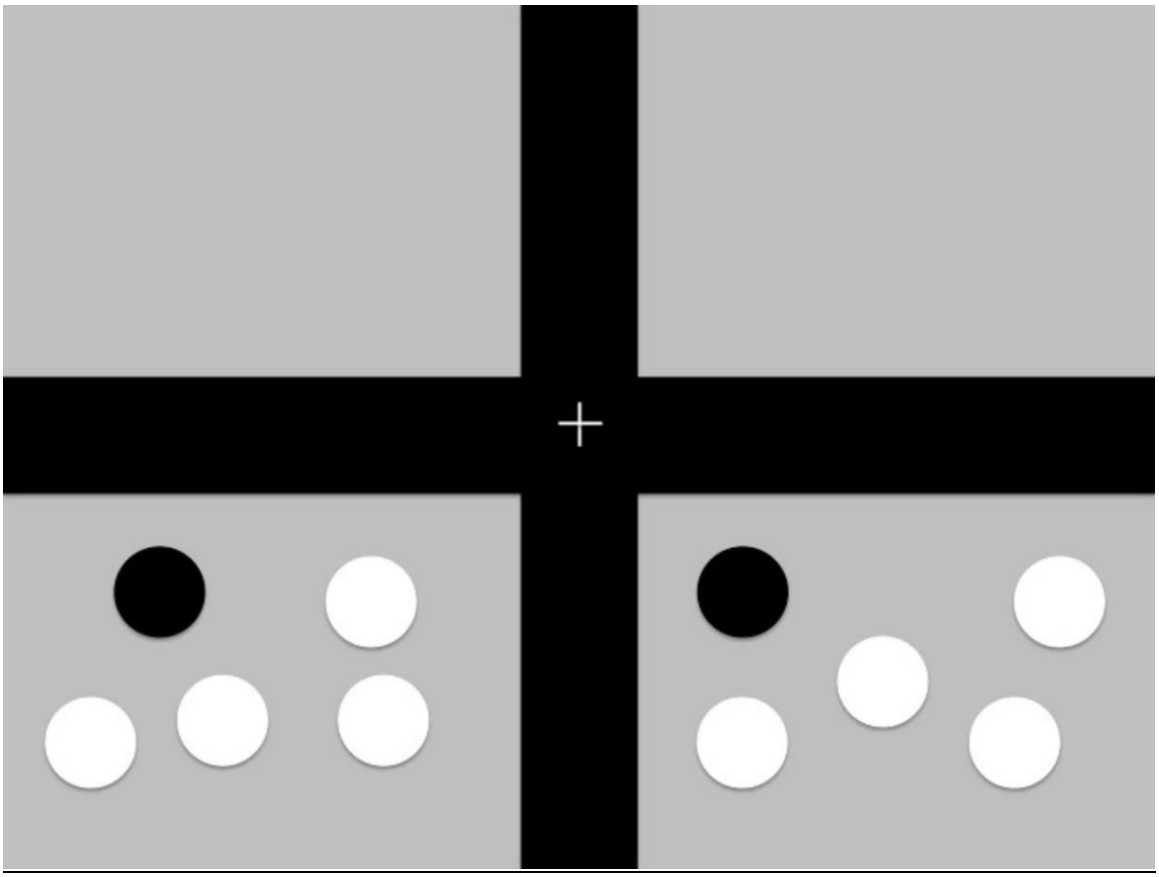

Figure 4-2. Bilateral condition – Two-target condition in the lower vertical hemifield.

Figures 4-1 and 4-2. Examples of the distribution of two targets on trial in the bilateral condition The objects were randomly distributed either in the upper or the lower vertical hemifield.

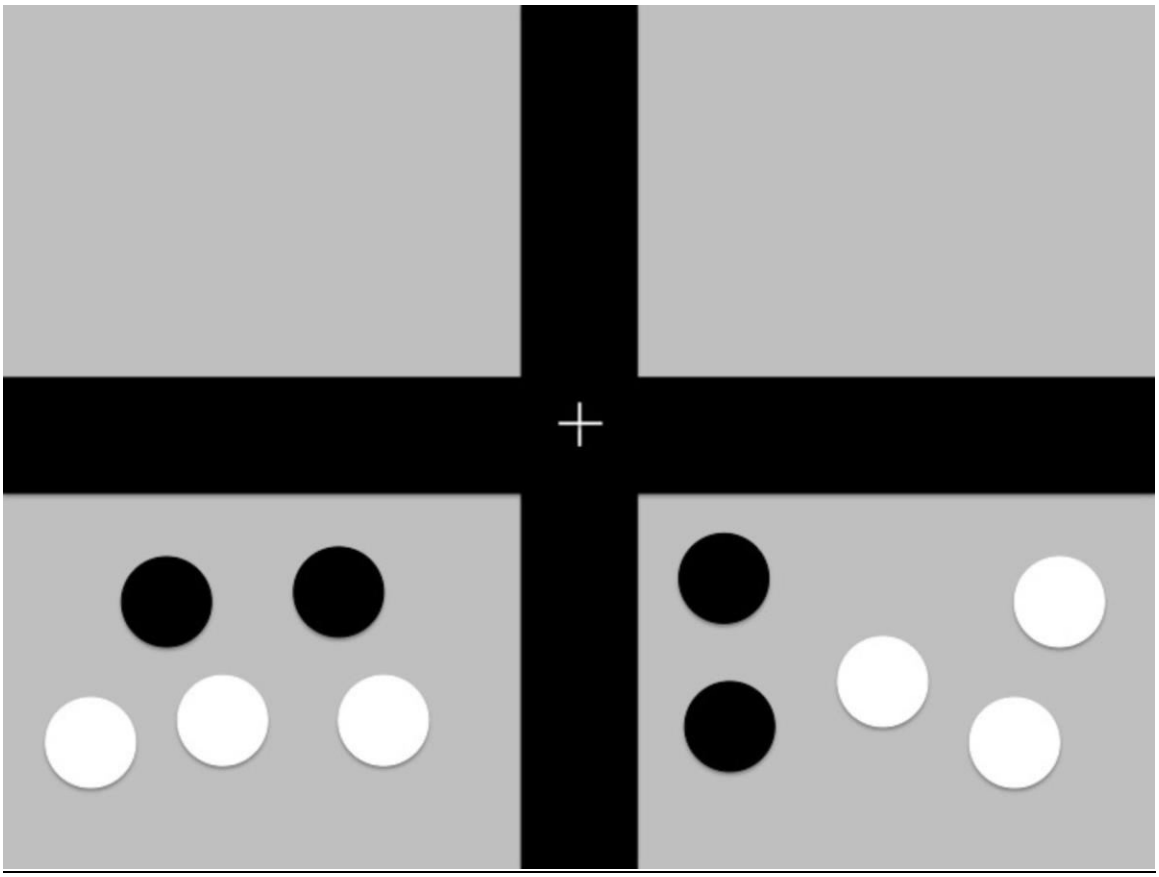

Figure 4-3. Bilateral condition – Four-target condition in the lower vertical hemifield.

.

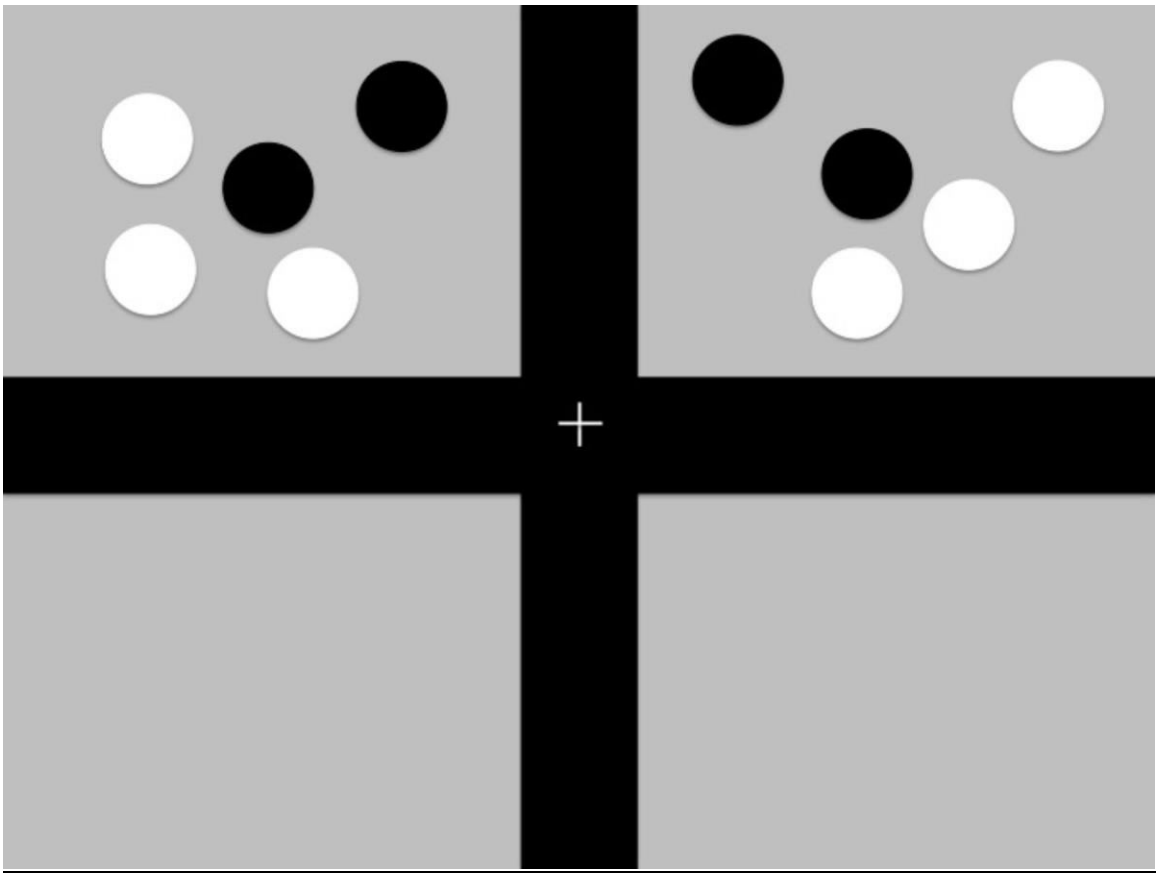

Figure 4-4. Bilateral condition – Four-target condition in the upper vertical hemifield.

Figures 4-3 and 4-4. Examples of the distribution of four targets on trials in the bilateral condition The objects were randomly distributed either in the upper or the lower vertical hemifield.

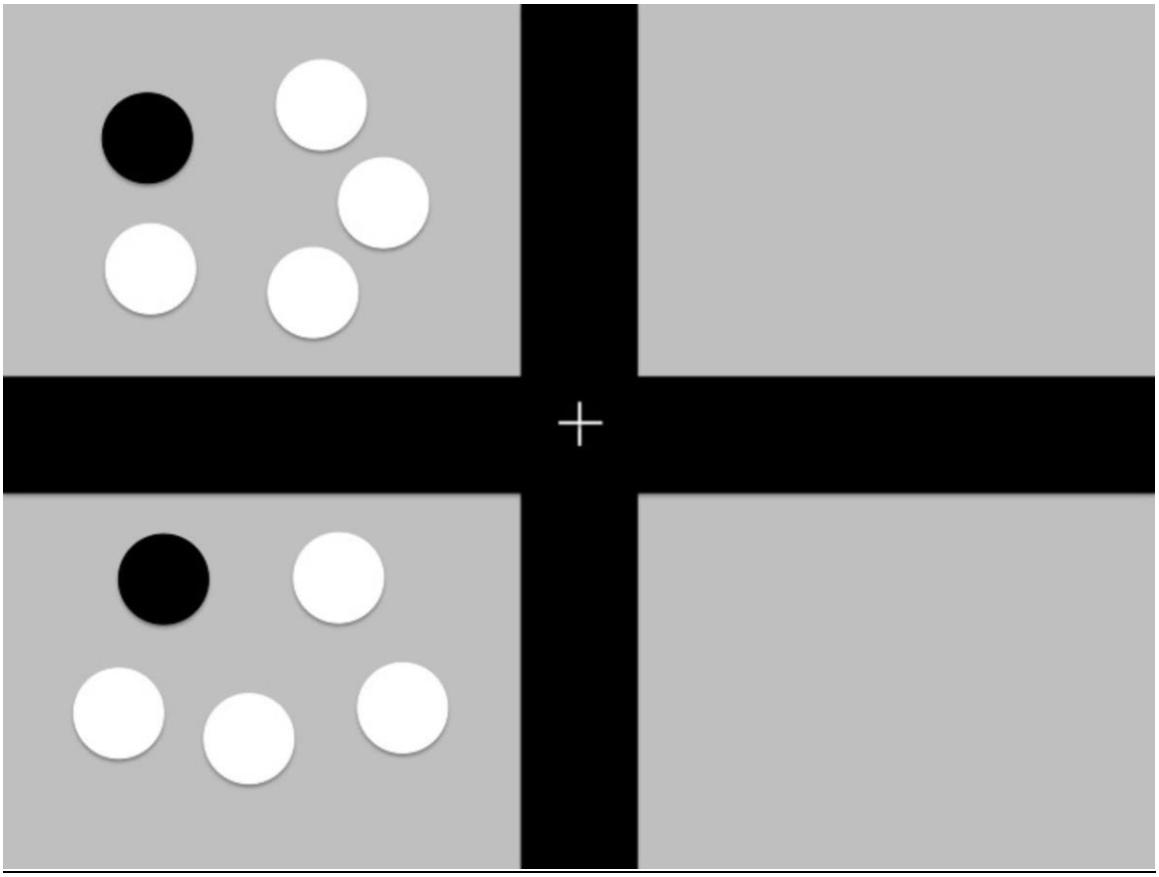

Figure 4- 5. Unilateral condition – Two-target condition in the left hemifield.

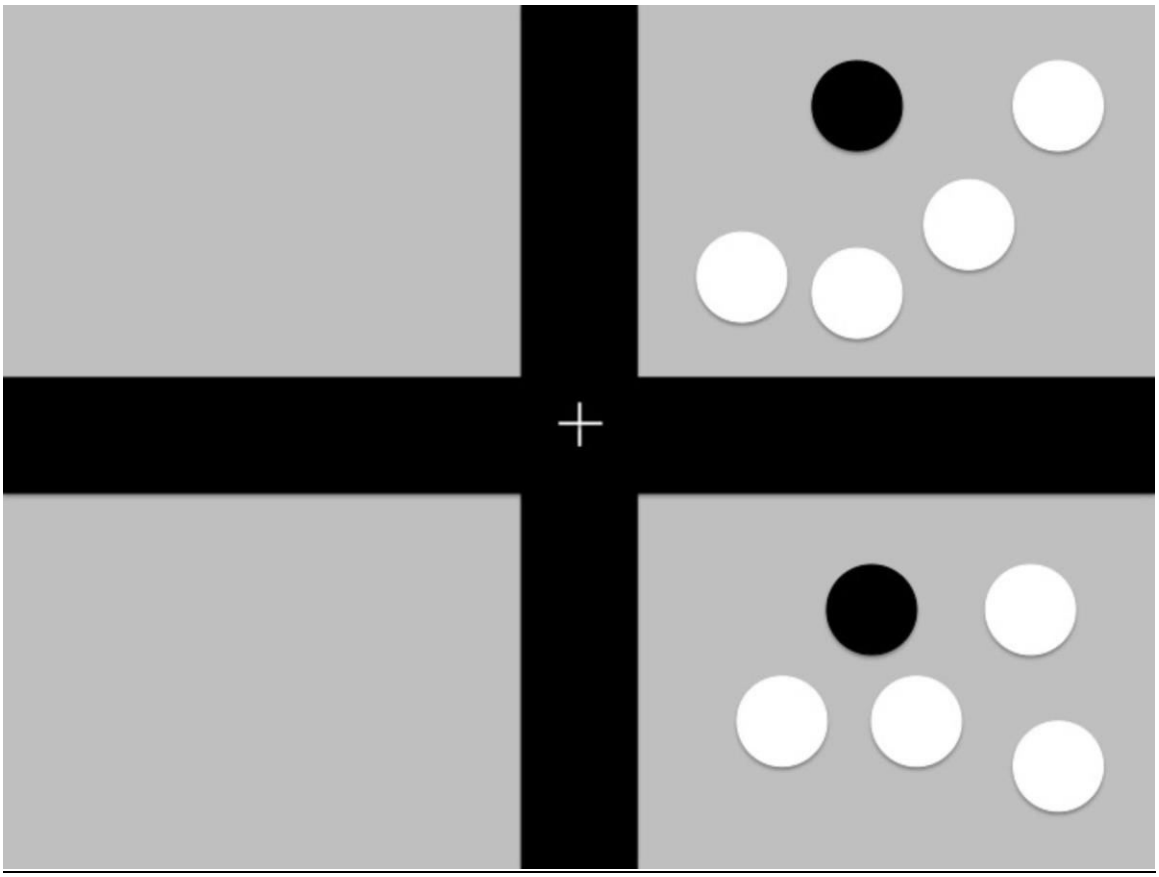

Figure 4- 6. Unilateral condition – Two-target condition in the right hemifield.

Figures 4-5 and 4-6. Examples of the distribution of two targets on trial in the unilateral condition. The objects were randomly distributed either in the left or the right hemifield.

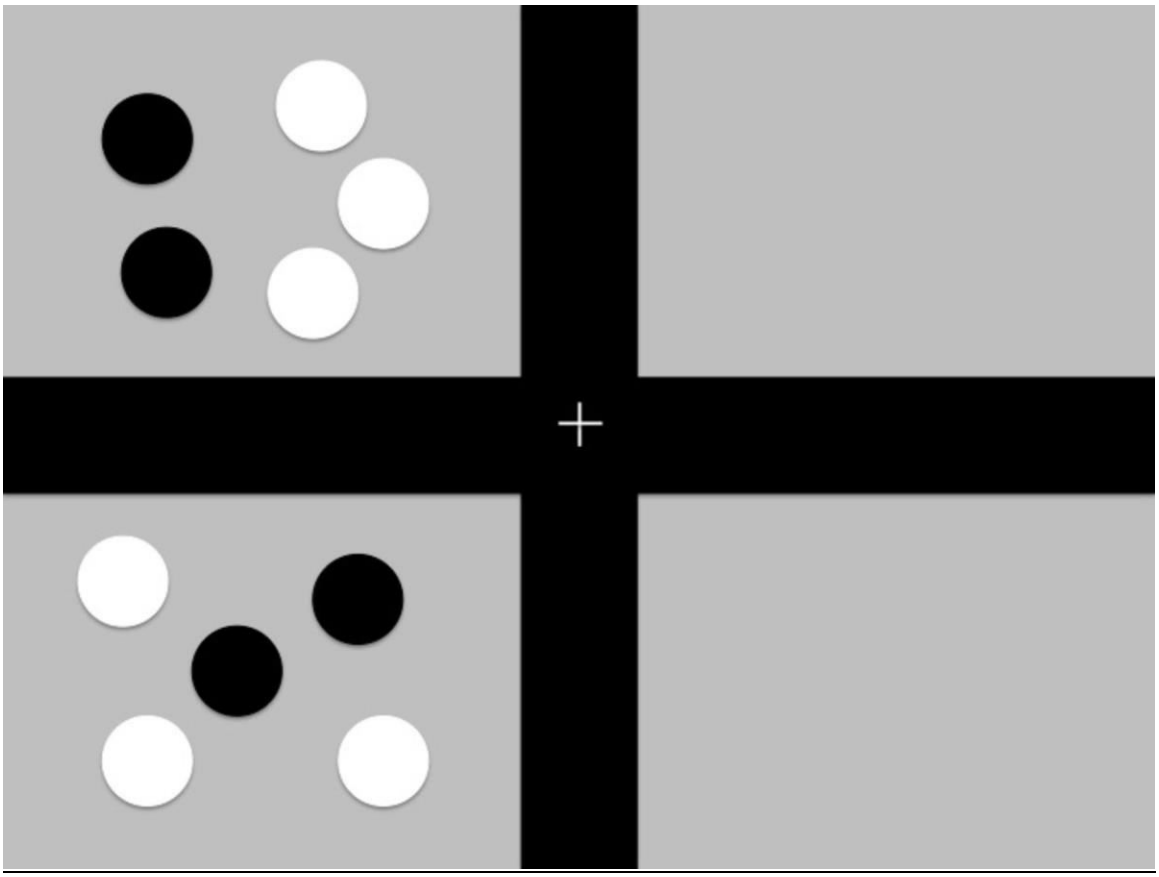

Figure 4-7. Unilateral condition – Four-target condition in the left hemifield.

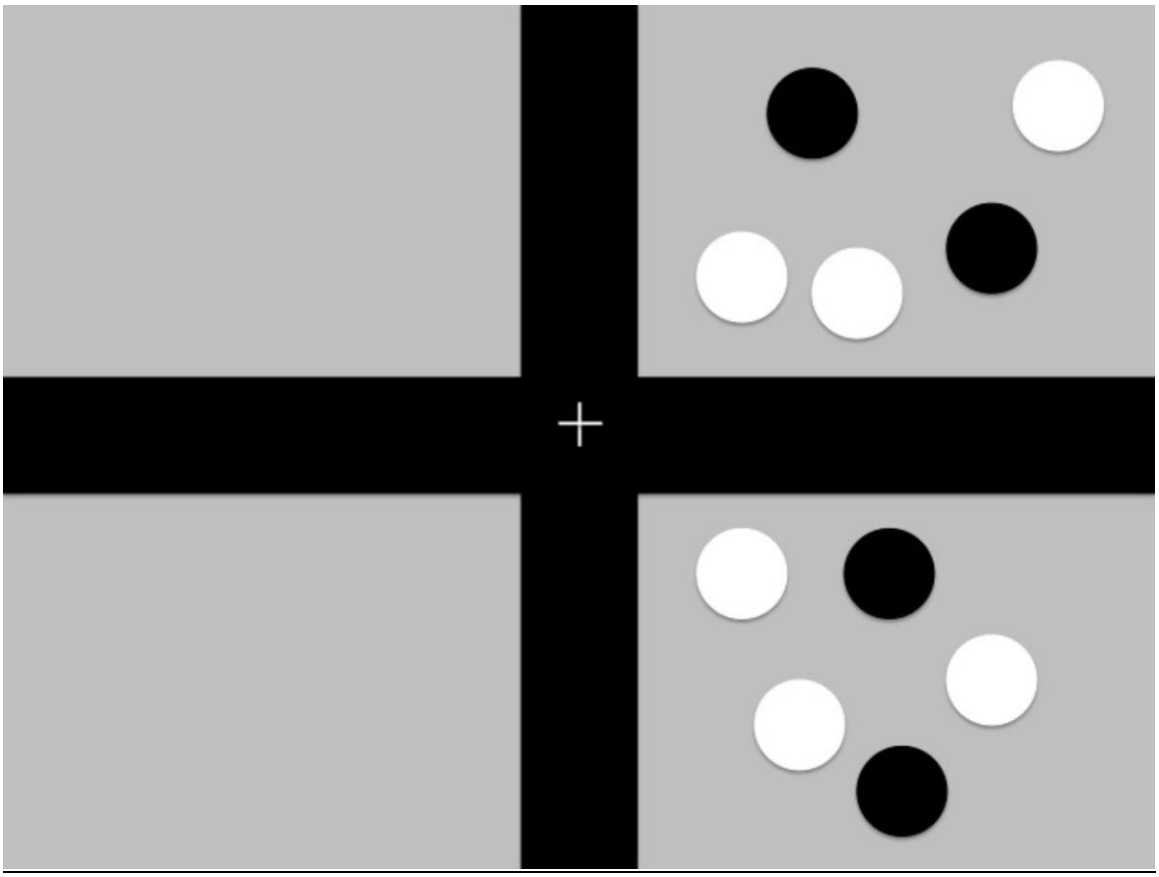

Figure 4-8. Unilateral condition – Four-target condition in the right hemifield.

Figures 4-7 and 4-8. Examples of the distribution of four targets on trials in the unilateral condition

The objects were randomly distributed either in the left or the right hemifield.

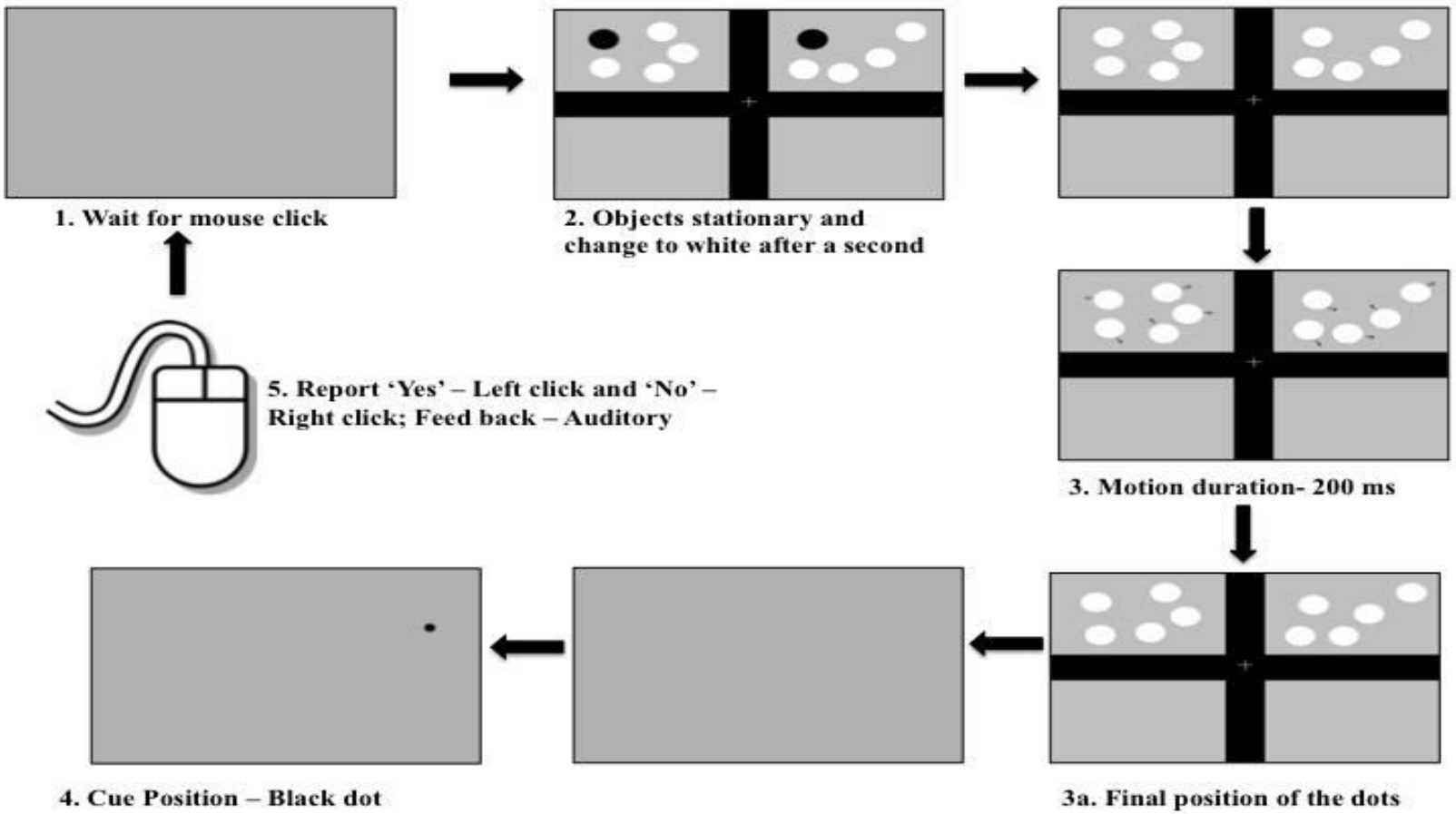

Figure 4- 9. Time sequence of a trial in experiment 3. Two targets or four targets with white distractors were displayed either in the right or left hemifields (unilateral condition) or in the upper or lower vertical hemifield (bilateral condition). The target's terminal position was cued by a black dot and the observers reported the whether the cued object was one among the initial group of black targets at the start of the trial.

4.2.3. Design:

Three replications X 20 trials X 2 target number conditions X 2 visual-field locations = 240 trials per subject. The order of target conditions (2 vs. 4) and visual-field locations was decided in a pseudo random order. In other words, unilateral and bilateral presentations and set size varied pseudo-randomly from block to block. The duration for each block of 20 trials was less than 3 min. Observers were given adequate breaks in between sessions.

4.2.4. Analysis:

The percentage of correct responses was calculated separately for trials containing two and four potential targets for the bilateral and unilateral visual-field conditions.

4.2.5. Predictions:

If there is a hemifield independence for the processing of moving objects, we would expect the performance in the bilateral condition to be better than the performance in the unilateral condition. This should be consistent for both the two- and four-potential-target conditions. Moreover, the performance in the two-target condition was expected to be better than the performance in the four-target condition.

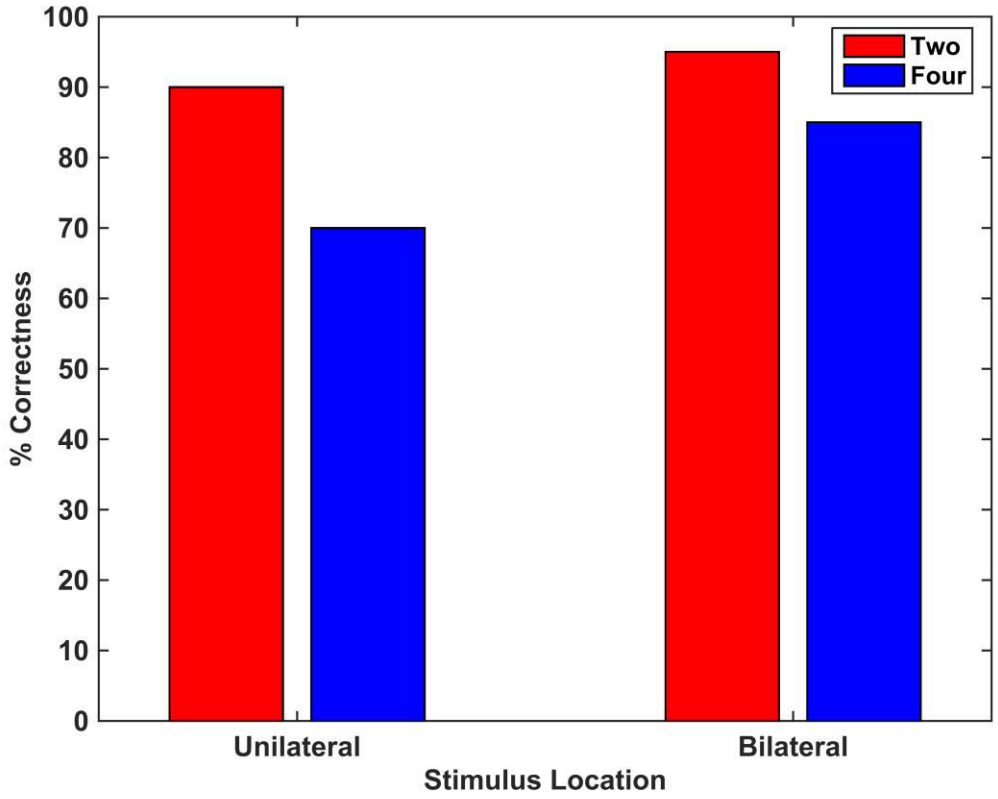

Figure 4- 10. Predicted performance for set size = 10. Two (red) and four potential targets (blue) are plotted for the unilateral and bilateral visual-field conditions.

4.2.6. Participants:

Pilot data were obtained for three observers for object set sizes 8 and 10. These pilot data were collected to determine an object-set size that would avoid both floor and ceiling effects. Based on the pilot data (See Appendix C), an object set size = 10 was chosen for the study.

Eight observers (25.8±2.3 years; Range: 24-30 years of age) with normal vision or corrected to normal vision, all of whom participated in the first experiment, were enrolled in this experiment. Experiments were conducted according to a protocol adhering to the Declaration of Helsinki and approved by the University of Houston Committee for the Protection of Human Subjects.

4.2.7. Data Analysis:

Data from eight observers were subjected to descriptive and inferential statistics using Microsoft Excel (2003) and STATA (StataCorp. 2015. *Stata Statistical Software: Release 14*. College Station, TX: StataCorp LP). Differences between performance in the bilateral and unilateral visual-field conditions were assessed using paired t tests. Significantly better performance in the bilateral condition for both the trials with two and four potential targets would be consistent with a hemifield independence for the deployment of attentional resources.

4.3. Results:

The correction for guessing was applied and the percent correct response was calculated for each subject. The correction was guessing was calculated using the formula:

P (corrected probability) = [P (raw probability) - chance] / [1- chance], where raw probability is the observed percentage of correct responses and the chance level is 0.2 for two targets and 0.4 for four targets.

The average percentage of correct responses across all observers was calculated for two and four potential targets in both the bilateral and unilateral visual-field conditions.

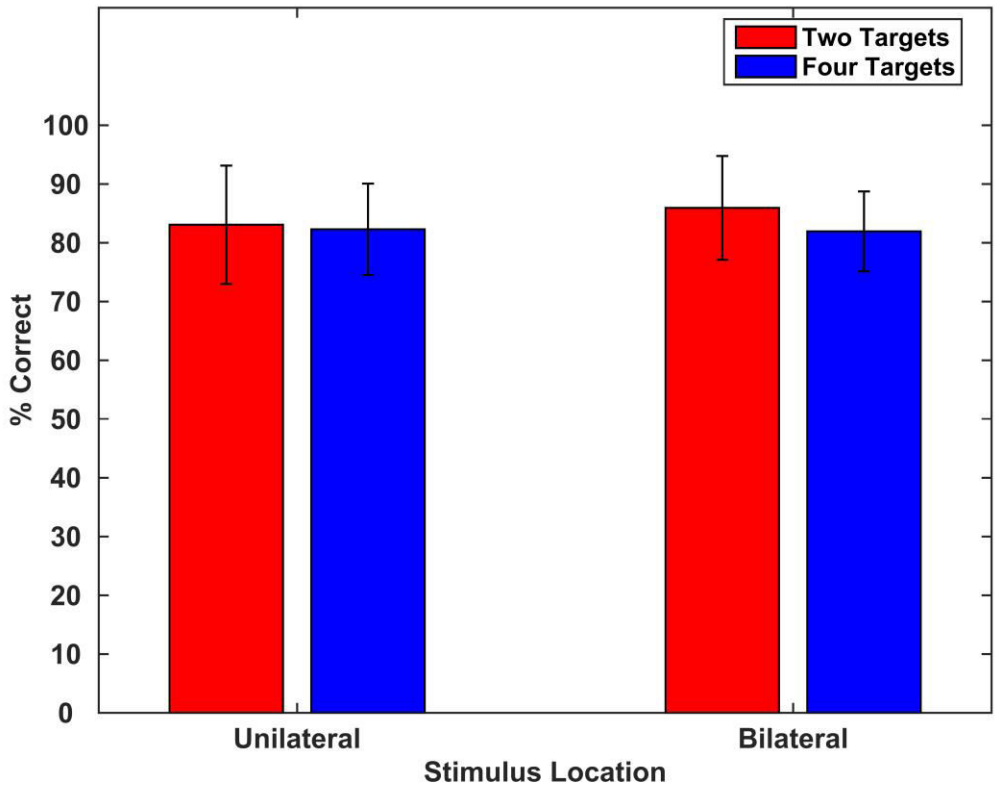

Figure 4- 11. Average measured performance for set size = 10. Results are shown for two (red) and four potential targets (blue) in the unilateral and bilateral visual-field conditions. Error bars: ±SEM.

Performance in the bilateral condition (Mean ± SEM = 85.94 ± 8.8) was slightly better than the performance in the unilateral condition (Mean ± SEM = 83.07 ± 10.0) when the display contained two potential targets. However, there was no difference in the performance between the bilateral (Mean ± SEM = 81.94 ± 6.8) and unilateral conditions (Mean ± SEM = 82.29 ± 7.8) in the four potential-target condition.

A paired-samples t-test was conducted to compare the performance in unilateral and bilateral conditions for two-targets. There was not a significant difference between the performance for the unilateral and bilateral conditions ($t[7]= 1.01$, $p = 0.346$).

A paired-samples t-test was conducted also to compare the performance in unilateral and bilateral visual-field conditions for trials with four potential targets. There also was not a significant difference in the performance for unilateral conditions ($t[7]= -0.143$, $p = 0.890$).

There was approximately a 1% *drop* in the performance for trials with four potential targets compared to two targets in the unilateral condition. Performance dropped 4% for trials with four and two potential targets in the bilateral condition.

A paired-samples t-test was conducted to compare the performance for two targets and four targets in the unilateral visual field condition. There was not a significant difference in the performance for two and four targets in the unilateral condition ($t [7]= 0.2120$, $p = 0.8381$).

Similarly, a paired-samples t-test was conducted to compare the performance for two targets and four targets in the bilateral visual-field condition. There was not a significant difference in the performance for two and four targets in the bilateral condition ($t [7]= 1.2572$, $p = 0.2490$). (See Appendix C for individual subjects' data)

4.4. Discussion:

In experiments 1 and 2, I found minimal or nil evidence for a bilateral advantage in motion information processing. I tried to replicate Alvarez and Cavanagh's study (2005) using my experimental set up in experiment 3. Many studies reported that performance in visual processing is better when the targets are presented in both hemifields compared with the targets presented in only one hemifield (Luck et al., 1989; Sereno et al., 1991; Alvarez and Cavanagh., 2005 and 2012).

I did not find any evidence of a bilateral advantage in my attempted replication of this earlier work. Alvarez and Cavangah (2005) used a set size of eight whereas I used a set size of ten. I did a pilot run on three subjects using a set size of eight (Refer to Appendix C) and the performance was greater than or equal to 90% in all trials. I ruled out this set size, the rationale being to avoid any ceiling effects on the performance. I chose a set size of ten because the performance of the subjects was well within the range of ceiling and floor effects. I did not try set sizes larger than 10 due to the limitations in the size of the display.

Alvarez and Cavanagh's experiment included 8 moving objects, two or four of which were marked as potential probe targets at the start of the trial. Their objects moved at 15° per second for 5 seconds and changed direction whenever they encountered other objects or edges. In my experiment, the speed of the target was 3° per second for a duration of 200 ms. In my experiment, objects did not hit the edges of the display or other nearby objects. Motion direction of the objects remained the same for 200 ms, unlike the Alvarez and Cavanagh's study.

The attentional tracking task used by Alvarez and Cavanagh might be more difficult than my task, with a higher speed and longer duration of motion along with the changes in the motion direction during each trial. These differences may account for the failure to find an advantage for bilaterally distributed targets in my study. However, Alvarez' & Cavanagh's observers performed at ~90% correct except for the unilateral condition with 4 potential targets, which is similar to the performance of my observers.

The targets in my study were marked as black and, when they turned white, moved only for 200 ms at 3° per second, corresponding to a displacement of 0.6 degrees. There can also be a possibility of a negative after-image from the 1-s pre-motion exposure afforded to my subjects, which may have allowed them to more readily identify targets during and after the period of motion.

Another possible reason for not getting similar results as in Alvarez and Cavanagh's study is the design of the experiment. It appears that Alvarez and Cavanagh interleaved the unilateral- and bilateral-condition within the same set of trials, whereas in my study the unilateral- and bilateral-condition trials were presented in separate blocks.

4.5 Conclusion:

The results of the attempt to replicate the study of Alvarez and Cavanagh (2005) indicate that I did not find any advantage of bilaterally distributed targets for object tracking. This lack of support for the previous findings may be attributable to differences in the experimental design of our study.

5. General Conclusions:

One of the research questions of this work was to investigate whether there are any independent attentional resources in hemifields in visual motion processing at stimulus encoding stage, sensory memory stage, and VSTM stage. The experimental design was similar to the study by Huynh et al., 2015. The first experiment was designed to investigate the stimulus encoding stage. The outcome of this experiment suggests that the performance in reporting direction when position information was cued decreased as a function of set size. This shows that a bottle-neck of visual processing occurs prior to the VSTM stage, at the stimulus encoding stage. The result that the stimulus encoding stage acts as a bottle-neck in visual processing is consistent with the previous findings reported by Ogmen et al., (2013) and Huynh et al., (2015). The drop in performance that I observed was consistent for unilateral and bilateral conditions. There was no difference in the performance for the unilateral and bilateral visual-field conditions as a function of set size. The absent of a significant difference between the performance in the unilateral and bilateral conditions suggests that no bilateral advantage for information processing exists at the stimulus encoding stage, which is a novel finding.

The second experiment was aimed at investigating whether attention has independent resources in the two hemifields at the sensory memory stage and the VSTM stage. The task of the subjects was similar to the first experiment, in which the subjects reported the direction of the object when position information was cued. The performance declined very little as a function of cue delay and performance was similar in both the unilateral and bilateral visual-field conditions. Thus, the results indicated no clear exponential

decay of sensory memory followed by a steady asymptotic VSTM, as had been reported in various studies (Sperling, 1960; Shooner et al., 2010; Bradley and Pearson, 2012; Ogmen et al., 2013). Although the results of my experiment did not show any exponential decay, the drop in performance for the one subject tested was more when tested using a larger set size, presumably beyond the capacity limits of VSTM (Pylyshyn and Storm., 1988; Luck and Vogel., 1997; Cowan, 2001). Of the previous studies that showed evidence for a decay of sensory memory, Shooner et al. (2010) used 9 items, Ogmen et al. (2013) used 5 and 9 items, and Bradley et al. (2012) used 10 items. The data collected for one subject using my experimental paradigm and a set size of 6 (Refer to Appendix B.2) suggests that the lack of an exponential drop in experiment 2 was due to the choice of small N = 2) and large (N = 4) set sizes that were within the capacity limit.

Another result of this experiment was there was no significant bilateral advantage at the VSTM stage but there was minimal bilateral advantage at the sensory memory stage. The finding of no bilateral advantage seen at the VSTM stage seems to contradict previous findings (Delvenne. 2005; Delvenne et al., 2011; Delvenne and Holt, 2012). However, the small statistically significant advantage seen at the sensory memory stage might be due to greater statistical power than at VSTM, after pooling of the results of the 5 shortest cue delays.

Existence of a bilateral advantage has been observed in a number of visual tasks, such as tracking objects (Alvarez and Cavanagh, 2005), remembering spatial locations (Delvenne, 2005) and orientations (Umemoto et al., 2010), and matching stimuli (Kraft et al., 2004; Sereno and Kosslyn, 1991). Hudson et al. (2012) attempted to replicate Alvarez and

Cavanagh (2005) in one of their experiments and found that hemifield independence was partial and not complete for object tracking. Upon considering these results, it is clear that a bilateral advantage is task specific and for object tracking it was not consistently reported. In my study, tracking accuracy was marginally better for the bilateral condition than the unilateral condition at the sensory memory stage, as well as at VSTM stage. Better tracking accuracy in the bilateral condition was seen for set sizes 2, 4, and 6 (data of one subject). Nonetheless, the finding of a minimal bilateral advantage in visual motion processing is a new finding.

The results of the first and the second experiment didn't explicitly show a bilateral advantage as reported in Alvarez and Cavanagh (2005). I tried to replicate Alvarez and Cavanagh (2005) with the same experimental paradigm used for experiments 1 and 2. Performance in the bilateral condition was better than the unilateral condition for the two-target condition, but not for the four-target condition. Therefore, the results of this experiment did not replicate the findings of Alvarez and Cavanagh (2005). Differences in the speed of the targets, the duration and course of motion, and in the experimental design might be reasons for the failure to replicate the results of Alvarez and Cavanagh (2005).

If there is an advantage in presenting targets to both hemifields, I would have expected to modify the existing leaky flask model. If there had been a bilateral advantage, I would have replaced the existing leaky flask model with two leaky flasks. One leaky flask would be wider at the top than the other according to the locations of targets in the visual field, i.e. unilateral or bilateral. In other words, one leaky flask model with a wider top

would have applied when the stimuli were distributed bilaterally and a second leaky flask with a narrower top would have applied if all the stimuli were unilateral.

From my results, I found no significant bilateral advantage in motion information processing. Hence, the existing leaky flask model remains intact. Based on the combined results of all the experiments, I conclude that attentional resources in the two hemifields might not be always independent for motion processing tasks when position information is used as a cue. However, this conclusion might not apply for motion processing tasks using other dimensions, such as color, as cue.

6. References:

Alvarez G.A., Cavanagh P. The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychol Sci.* 2004; 15(2):106-111.

Alvarez G.A., Cavanagh P. Independent resources for attentional tracking in the left and right visual hemifields. *Psychol Sci*. 2005 Aug; 16(8): 637-643.

Alvarez G.A., Gill J., Cavanagh P. Anatomical constraints on attention: hemifield independence is a signature of multifocal spatial selection. *J Vis*. 2012 May 25; 12(5): 9:1-20.

Arguin M., Joanette Y., Cavanagh P. Comparing the cerebral hemispheres on the speed of spatial shifts of visual attention: evidence from serial search. *Neuropsychologia*. 1990; 28(7):733-736

Averbach, E., Coriell, A. S. Short-term memory in vision. *Bell Systems Technical Journal*, 1961. 40, 309-328.

Awh E., Pashler H. Evidence for split attentional foci. *J Exp Psychol Hum Percept Perform*. 2000 Apr; 26(2): 834-846.

Awh E., Vogel E. K., and Oh S. Interactions between attention and working memory. *Neuroscience*. 2005 139, 201–208.

Bays P.M., Catalao R.F., Husain M. The precision of visual working memory is set by allocation of a shared resource. *J Vis*. 2009 Sep 9; 9(10): 7.1-11.

Blake R., Cepeda N.J., Hiris E. Memory for visual motion. *J Exp Psychol Hum Percept Perform.* 1997; 23(2): 353-369.

Bradley C., Pearson J. The sensory components of high-capacity iconic memory and visual working memory. *Front Psychol*. 2012; 3: 355:1-8.

Cowan N. The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behav Brain Sci*. 2001; 24(1): 87-114; discussion 114-185.

Delvenne J.F. The capacity of visual short-term memory within and between hemifields. *Cognition*. 2005; 96(3): B79-88.

Delvenne J.F., Kaddour L.A., Castronovo J. An electrophysiological measure of visual short-term memory capacity within and across hemifields. *Psychophysiology*. 2011; 48(3): 333-336.

Delvenne J.F., Holt J.L. Splitting attention across the two visual fields in visual short-term memory. *Cognition*. 2012 ; 122(2): 258-263.

Demkiw P., Michaels C.F. Motion information in iconic memory. *Acta Psychol (Amst)*. 1976; 40(4): 257-264.

Fougnie D., Marois R. Attentive Tracking Disrupts Feature Binding in Visual Working Memory. *Vis Cogn.* 2009; 17(1-2): 48-66.

Fukuda K., Awh E., Vogel E.K. Discrete capacity limits in visual working memory. *Curr Opin Neurobiol*. 2010; 20(2): 177-182.

Gegenfurtner K.R., Sperling G. Information transfer in iconic memory experiments. *J Exp Psychol Hum Percept Perform.* 1993; 19(4): 845-866.

Harasawa M., Shioiri S. Asymmetrical brain activity induced by voluntary spatial attention depends on the visual hemifield: a functional near-infrared spectroscopy study. *Brain Cogn*. 2011; 75(3): 292-298.

Hudson C., Howe P.D., Little D.R. Hemifield effects in multiple identity tracking. *PLoS One*. 2012;7(8):1-8.

Holt J.L., Delvenne J.F. A bilateral advantage in controlling access to visual short-term memory. *Exp Psychol.* 2014; 61(2): 127-133.

Holt J.L., Delvenne J.F. A bilateral advantage for maintaining objects in visual short term memory. *Acta Psychol (*Amst). 2015; 154:54-61.

Huynh D.L., Tripathy S.P., Bedell H.E., Ögmen H. Stream specificity and asymmetries in feature binding and content-addressable access in visual encoding and memory. *J Vis*. 2015; 15(13): 14;1-32.

Kraft A., Müller N.G., Hagendorf H., Schira M.M., Dick S., Fendrich R.M., Brandt S.A. Interactions between task difficulty and hemispheric distribution of attended locations: implications for the splitting attention debate. *Brain Res Cogn Brain Res*. 2005; 24(1): 19-32.

Kraft A., Kehrer S., Hagendorf H., Brandt S.A. Hemifield effects of spatial attention in early human visual cortex. *Eur J Neurosci.* 2011; 33(12): 2349-2358.

Lapierre M., Howe PD., Cropper S.J. Transfer of learning between hemifields in multiple object tracking: memory reduces constraints of attention. *PLoS One*. 2013; 8(12):1-16.

Luck S.J., Hillyard S.A., Mangun G.R., Gazzaniga M.S. Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature*. 1989; 342(6249): 543-545.

Luck S.J., Vogel E.K. The capacity of visual working memory for features and conjunctions. Nature. 1997; 390(6657): 279-281.

Macaluso E., Frith C. Interhemispheric differences in extrastriate areas during visuo-spatial selective attention. *Neuroimage*. 2000; 12(5): 485-494.

Magnussen S., Greenlee M.W., Asplund R., Dyrnes S. Stimulus-specific mechanisms of visual short-term memory. *Vision Res*. 1991; 31(7-8): 1213-1219.

Magnussen S., Greenlee M.W. Retention and disruption of motion information in visual short-term memory. *J Exp Psychol Learn Mem Cogn*. 1992; 18(1): 151-156.

Magnussen S., Greenlee M.W., Thomas J.P. Parallel processing in visual short-term memory. *J Exp Psychol Hum Percept Perform*. 1996; 22(1): 202-212.

Magnussen S., Greenlee M.W. The psychophysics of perceptual memory. *Psychol Res*. 1999; 62(2-3): 81-92.

Magnussen S. Low-level memory processes in vision. *Trends Neurosci*. 2000; 23(6): 247-251.

Makovsik T., Jiang Y.V. Distributing versus focusing attention in visual short-term memory. *Psychon Bull Rev*. 2007; 14(6): 1072-1078.

Narasimhan S., Tripathy S.P., Barrett B.T. Loss of positional information when tracking multiple moving dots: the role of visual memory. *Vision Res.* 2009; 49(1): 10-27.

Öğmen H., Ekiz O., Huynh D., Bedell H.E., Tripathy S.P. Bottlenecks of motion processing during a visual glance: the leaky flask model. *PLoS One*. 2013; 8(12): 1-12.

Oksama L., Hyönä J. Dynamic binding of identity and location information: a serial model of multiple identity tracking. *Cogn Psychol*. 2008 Jun;56(4):237-83.

Pasternak T., Zaksas D. Stimulus specificity and temporal dynamics of working memory for visual motion. *J Neurophysiol.* 2003; 90(4): 2757-2762.

Pasternak T., Greenlee M.W. Working memory in primate sensory systems. *Nat Rev Neurosci*. 2005; 6(2): 97-107.

Persuh M., Genzer B., Melara R.D. Iconic memory requires attention. *Front Hum Neurosci*. 2012; 6: 12:1-8.

Phillips, W.A., On the distinction between sensory storage and short-term visual memory, *Percept. Psychophys.*, 1974; 16: 283-290.

Proverbio A.M, Zani A, Avella C. Hemispheric asymmetries for spatial frequency discrimination in a selective attention task. *Brain Cogn*. 1997; 34(2)311-320.

Pylyshyn, Z. W., Storm, R. W. Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spat .Vision*. 1988; 3(3): 179–197.

Rhodes D.L., Robertson L.C. Visual field asymmetries and allocation of attention in visual scenes. *Brain Cogn.* 2002; 50(1): 95-115.

Sereno A.B., Kosslyn S.M. Discrimination within and between hemifields: a new constraint on theories of attention. *Neuropsychologia*. 1991; 29(7): 659-675.

Shooner C., Tripathy S., Bedell H., Öğmen H. High-capacity, transient retention of direction-of-motion information for multiple moving objects. *J Vis*. 2010, 10(6): 8, 1–20.

Sperling G. The information available in brief visual presentations. Psychological Monographs: General and Applied. 1960; 74 (11, Whole No. 498): 1–29.

Störmer V.S., Alvarez G.A., Cavanagh P. Within-hemifield competition in early visual areas limits the ability to track multiple objects with attention. *J Neurosci*. 2014; 34(35): 11526-11533.

Tripathy, S.P., Barrett, B.T. Severe loss of positional information when detecting deviations in multiple trajectories. *J. Vis*. 2004; 4(12): 4, 1020-1043.

Umemoto A., Drew T., Ester E.F., Awh E. A bilateral advantage for storage in visual working memory. *Cognition*. 2010; 117(1): 69-79.

Walter S, Keitel C, Müller M.M. Sustained Splits of Attention within versus across Visual Hemifields Produce Distinct Spatial Gain Profiles. *J Cogn Neurosci*. 2016; 28(1): 111-124

Zhang W., Luck S.J. Discrete fixed-resolution representations in visual working memory. *Nature* 2008; 453(7192): 233–235.

APPENDIX A

Appendix A.1 Individual Subjects' plots for experiment I

Average Transformed performance for each subject for the unilateral and bilateral conditions as a function of set size

In Appendix A.1, the average transformed performance for each subject in the bilateral and unilateral conditions is plotted as a function of set size. In the figures (A.1.1-1.9), performance drops as a function of set size. There is not much of a difference in performance between the unilateral and bilateral conditions, except for subjects VIG, SUY, and NGS.

Lines plotted in red denote the unilateral condition, lines plotted in blue denote the bilateral condition, and dashed lines in black denote performance at the chance level.

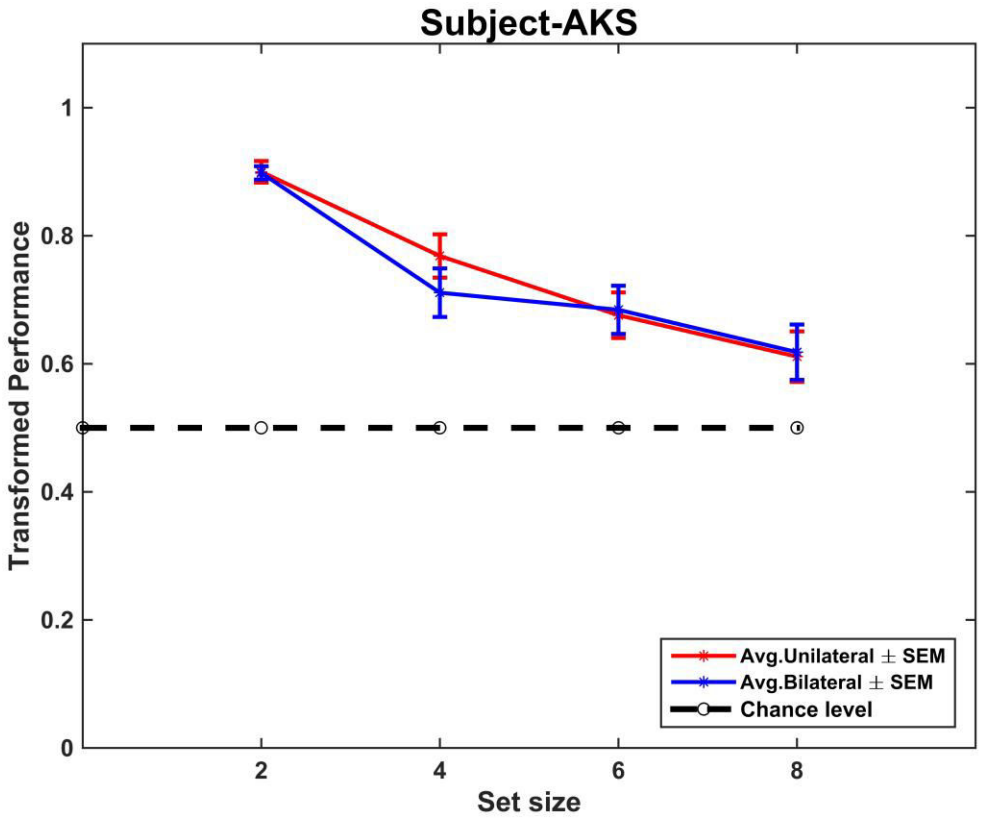

Figure A.1 1. Average transformed performance for subject AKS.

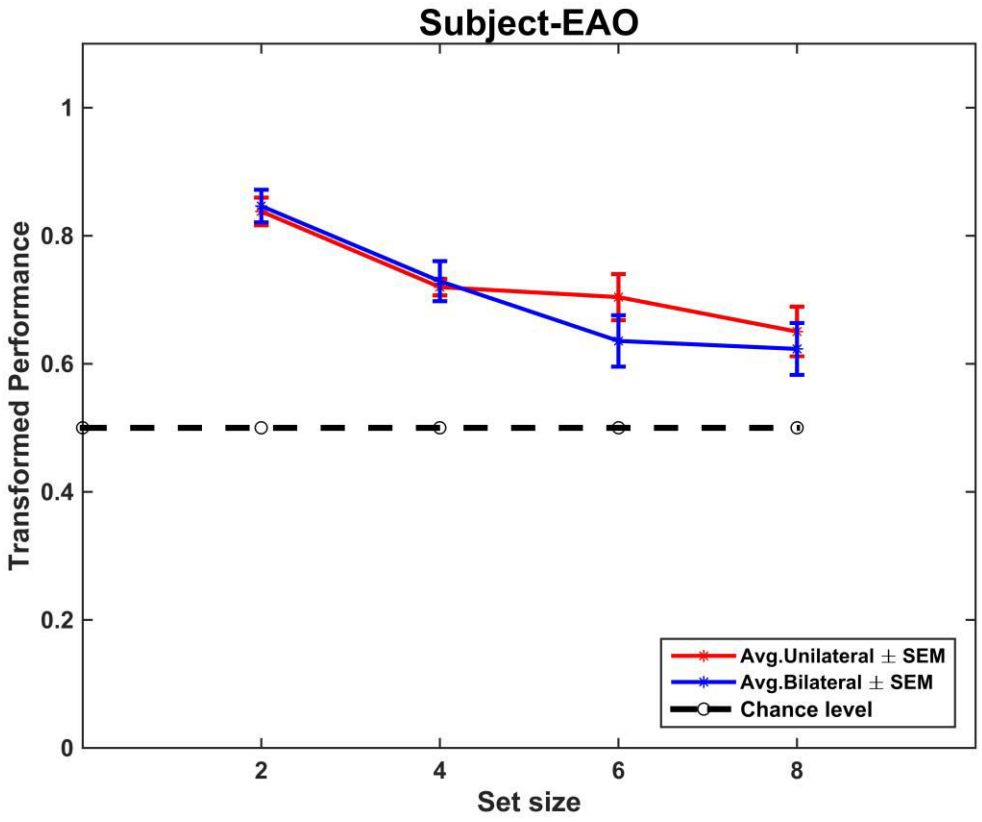

Figure A.1 2. Average transformed performance for subject EAO.

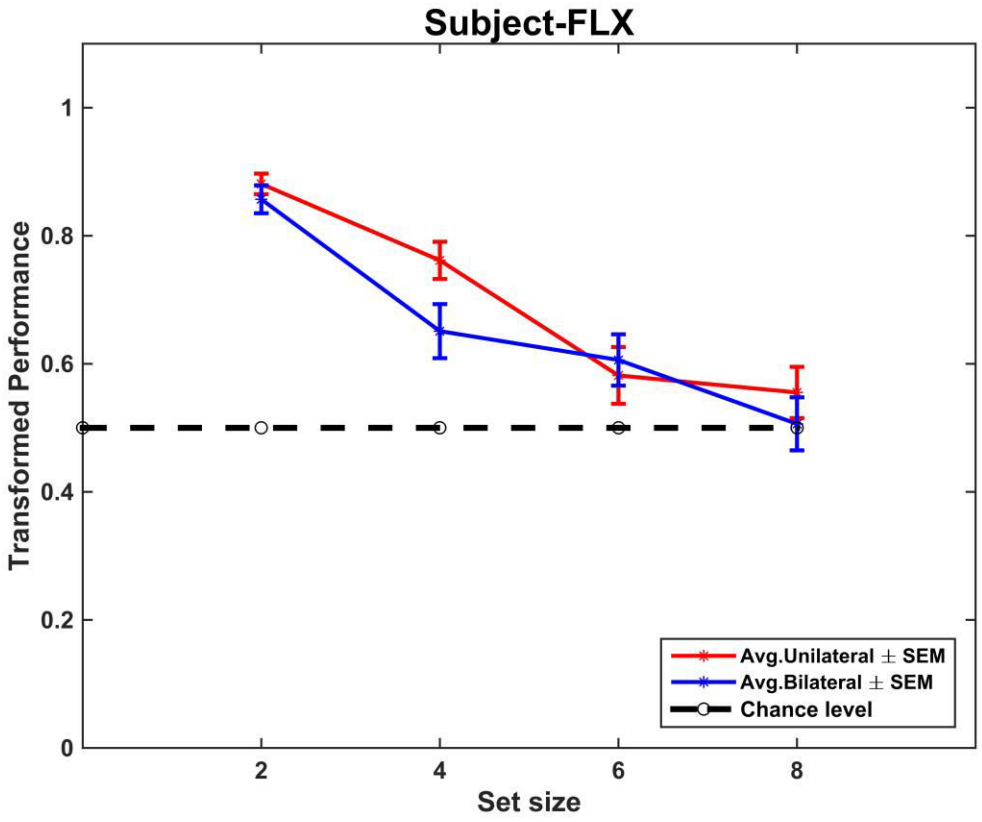

Figure A.1 3. Average transformed performance for subject FLX.

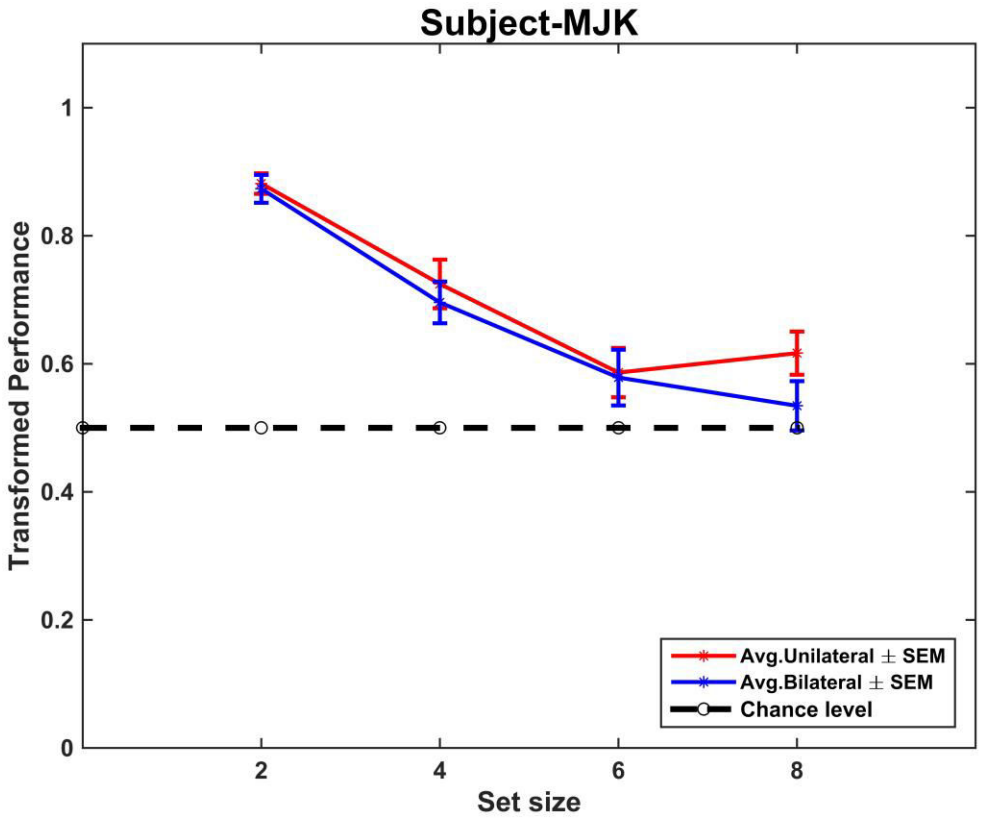

Figure A.1 4. Average transformed performance for subject MJK.

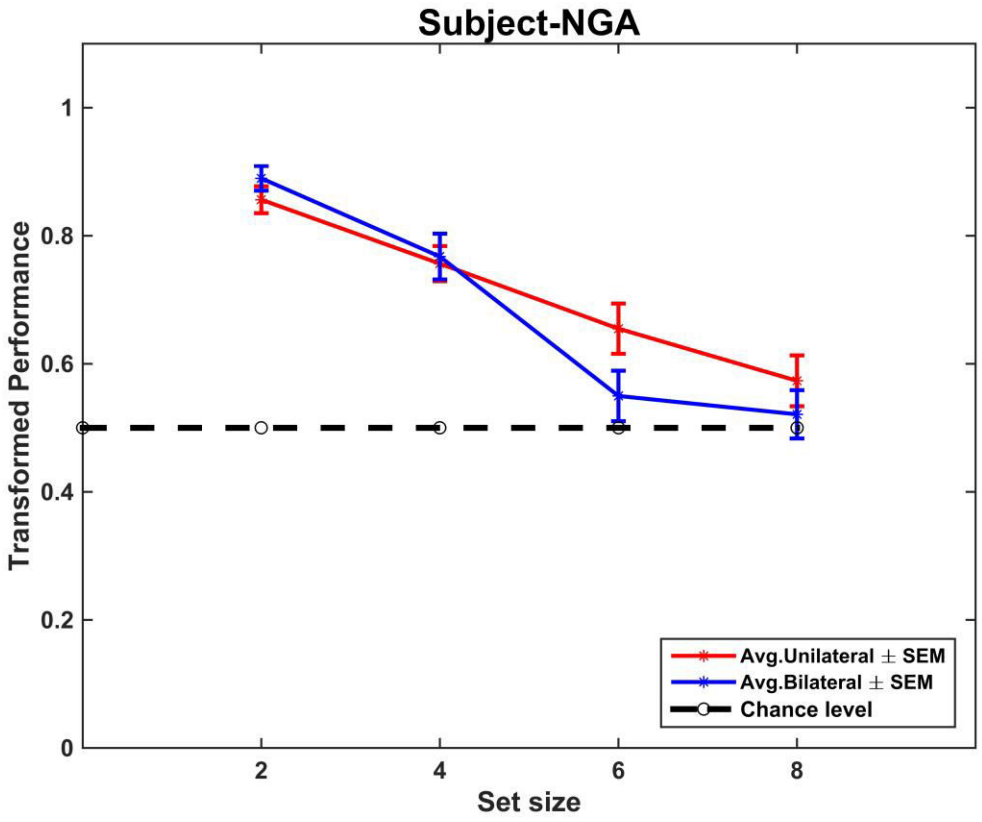

Figure A.1 5. Average transformed performance for subject NGA.

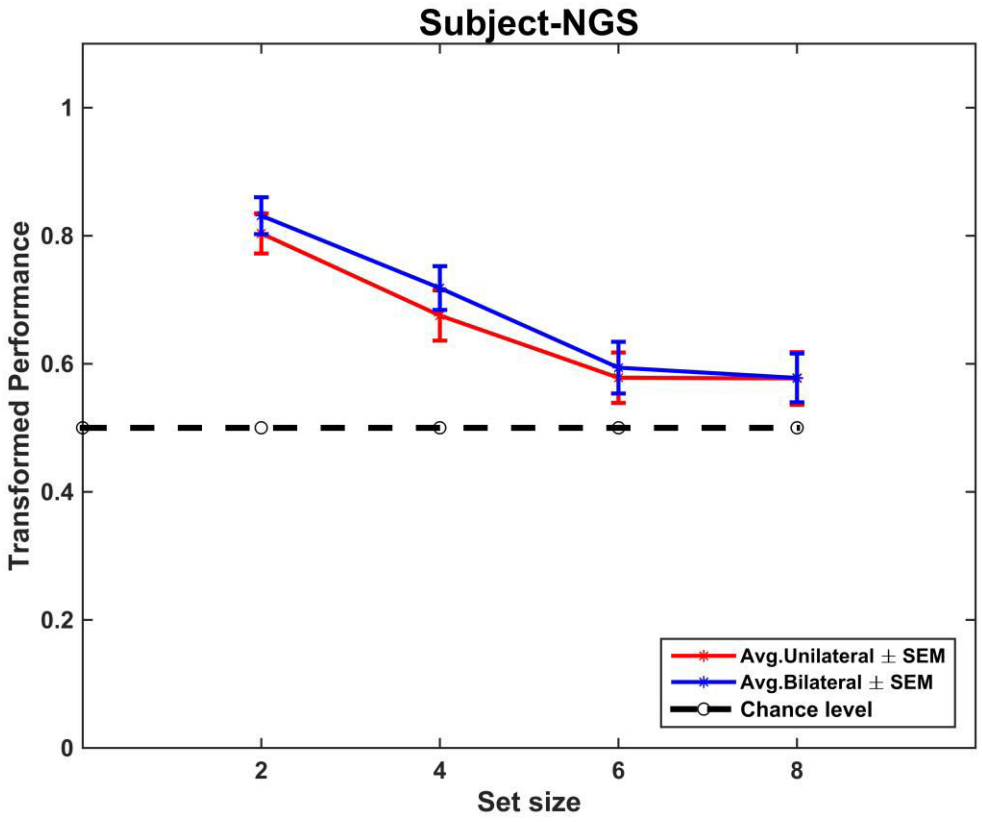

Figure A.1 6. Average transformed performance for subject NGS.

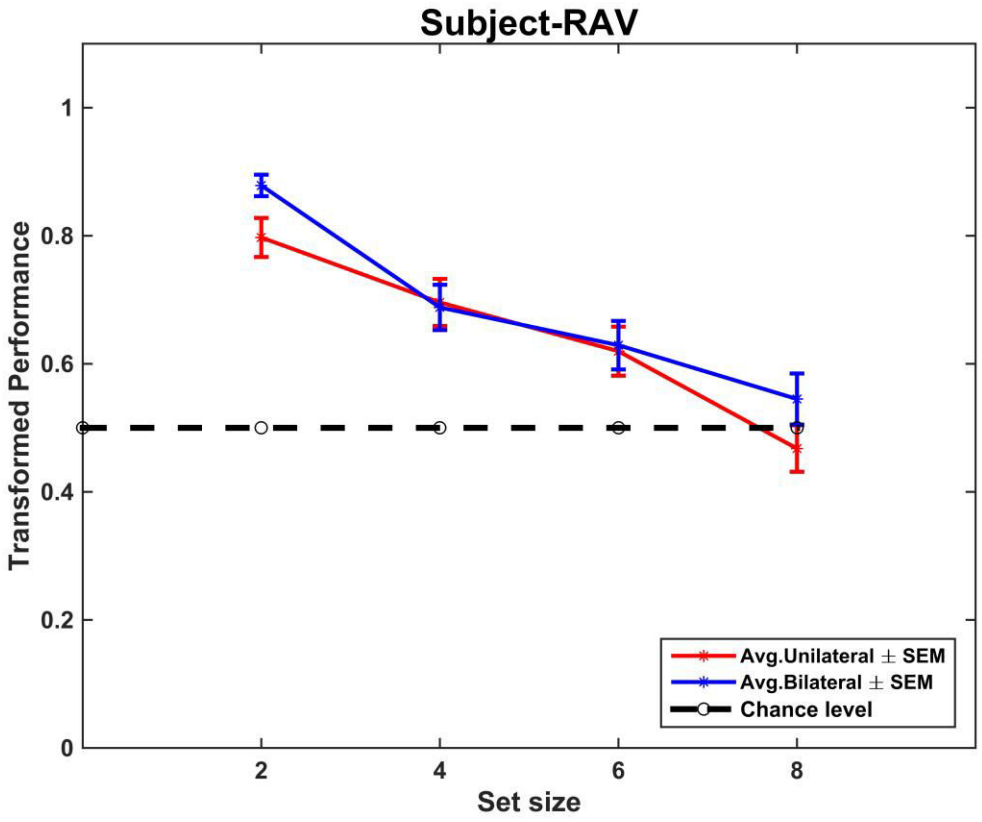

Figure A.1 7. Average transformed performance for subject RAV.

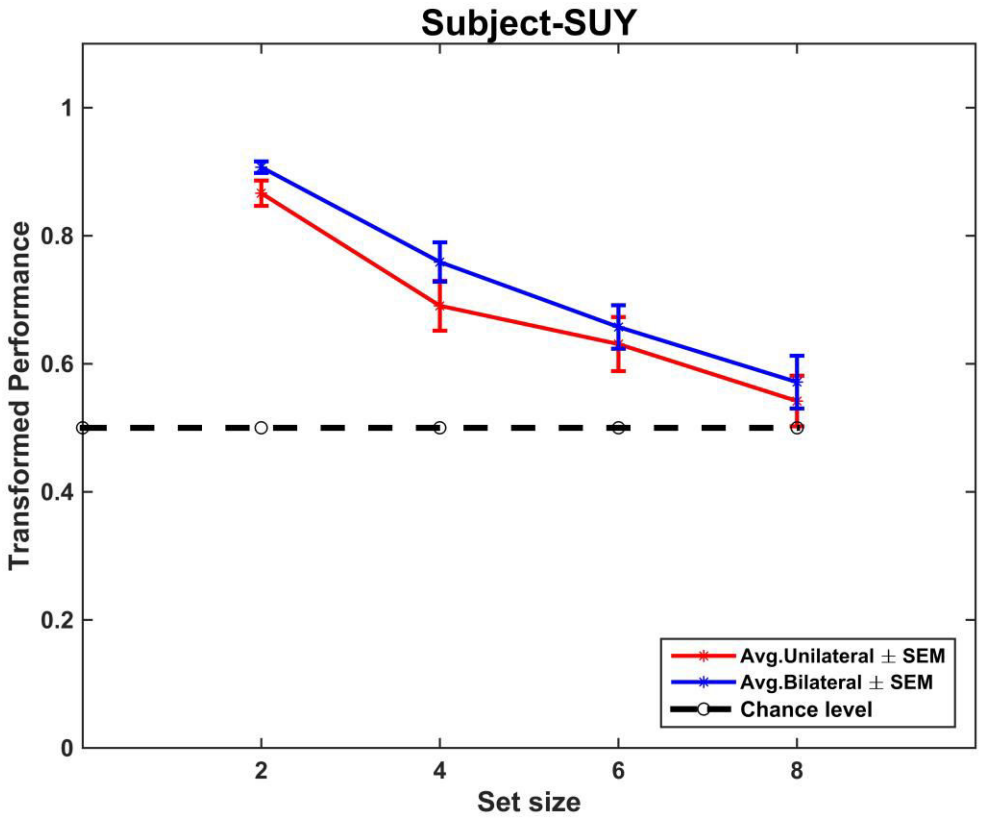

Figure A.1 8. Average transformed performance for subject SUY.

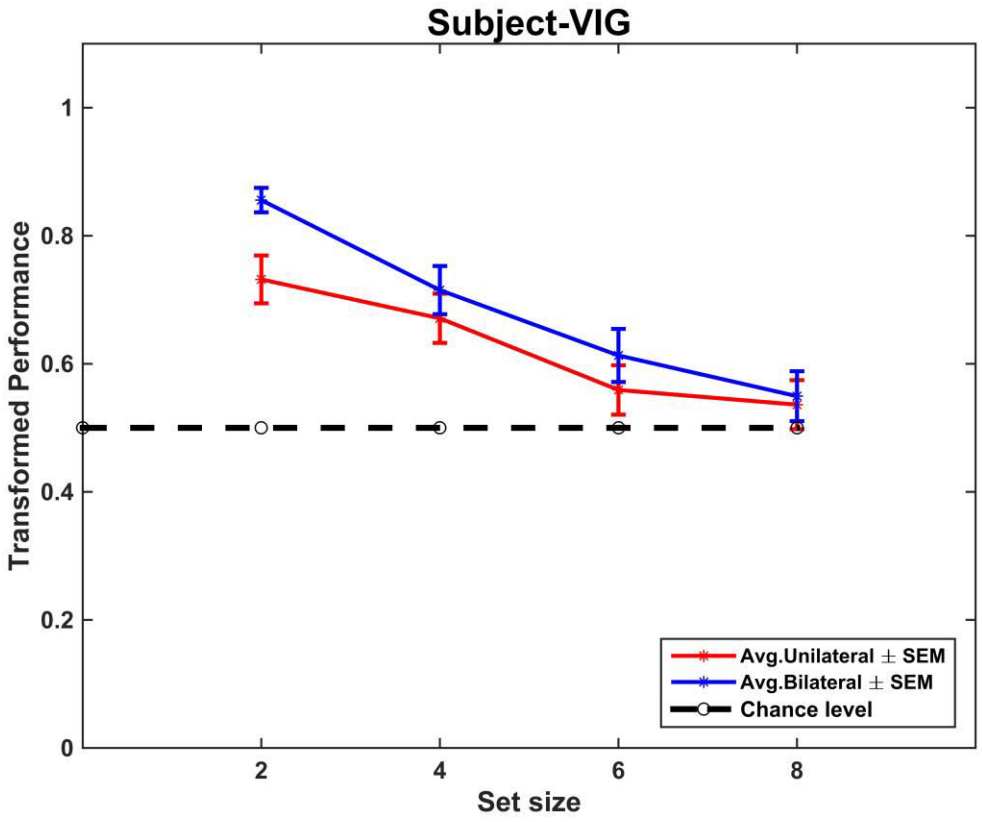

Figure A.1 9. Average transformed performance for subject VIG.

APPENDIX B

Appendix B.1 Individual Subjects' plots for experiment II

Average Transformed performance for each subject for the unilateral and bilateral conditions as a function of cue delay

In Appendix B.1, the average transformed performance for each subject in the bilateral and unilateral conditions for two set sizes is plotted as a function of cue delay. In the figures (B.1.1-1.8), performance drops minimally as a function of cue delay for most of the subjects. Performance for the smaller set size was better than for the larger set size in all subjects. This was consistent for both the unilateral and bilateral conditions.

Lines plotted in red denote the unilateral condition, lines plotted in blue denote the bilateral condition, and dashed lines in black denote performance at the chance level. Lines with star symbol represents the smaller set size and lines with open squares denote the larger set size.

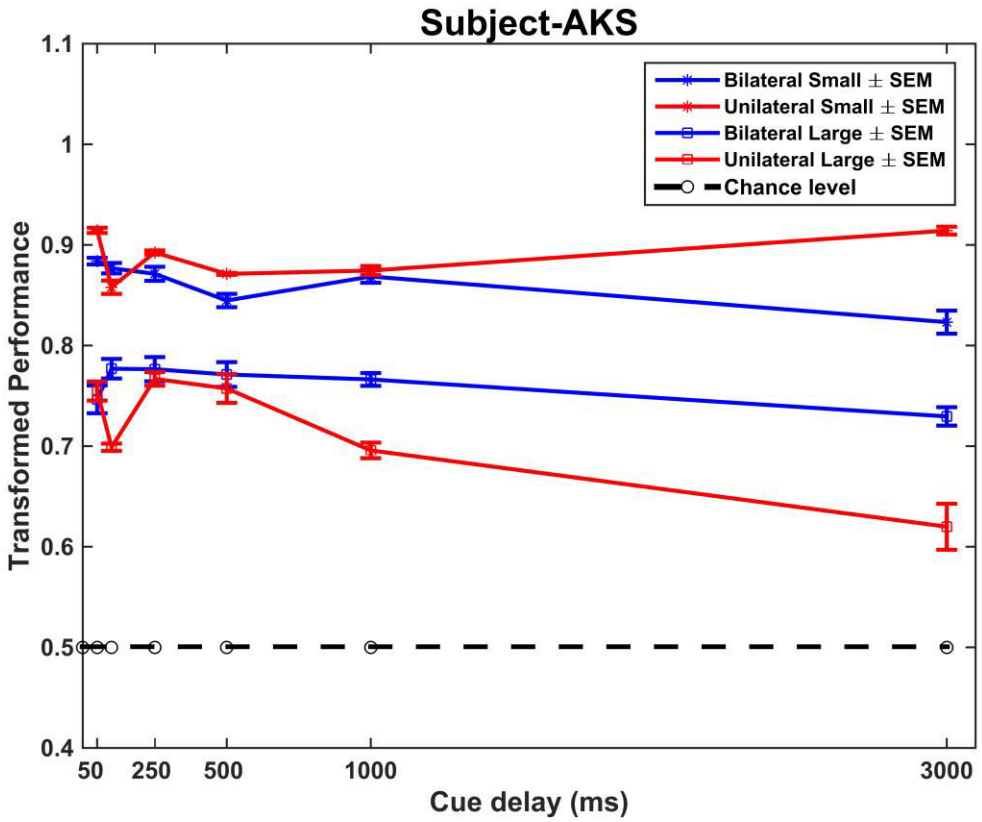

Figure. B.1. 1. Average transformed performance for unilateral small, unilateral large, bilateral small, and bilateral large set sizes for subject AKS.

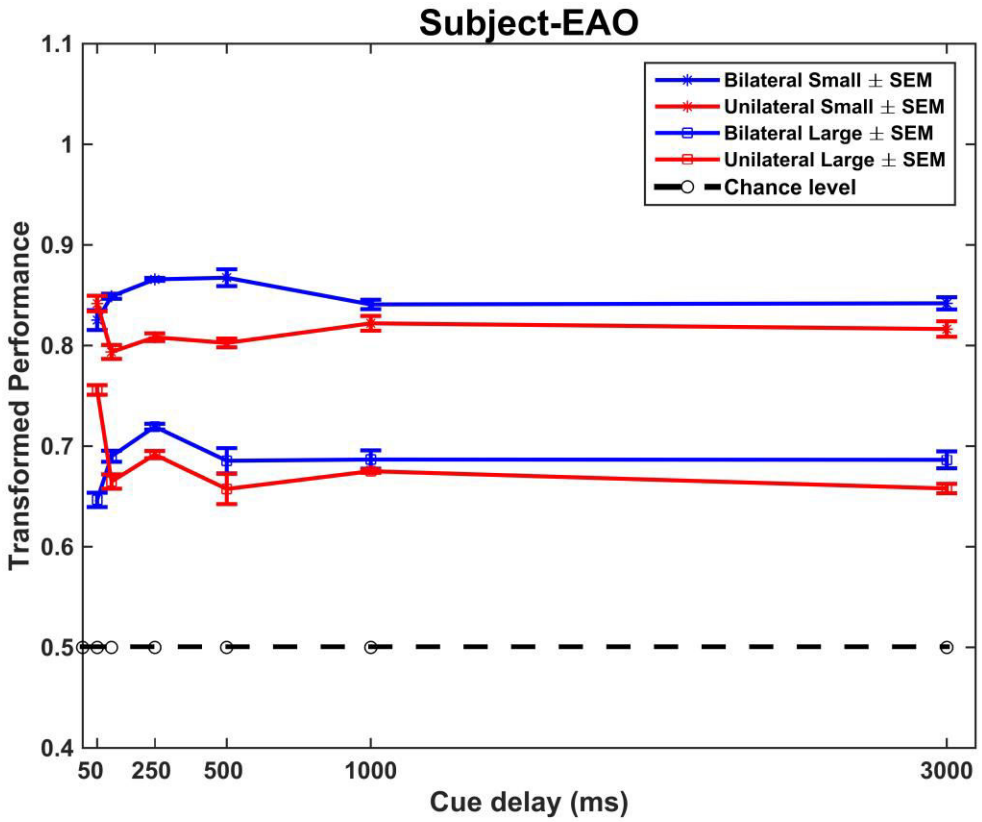

Figure. B.1. 2. Average transformed performance for unilateral small, unilateral large, bilateral small, and bilateral large set sizes for subject EAO.

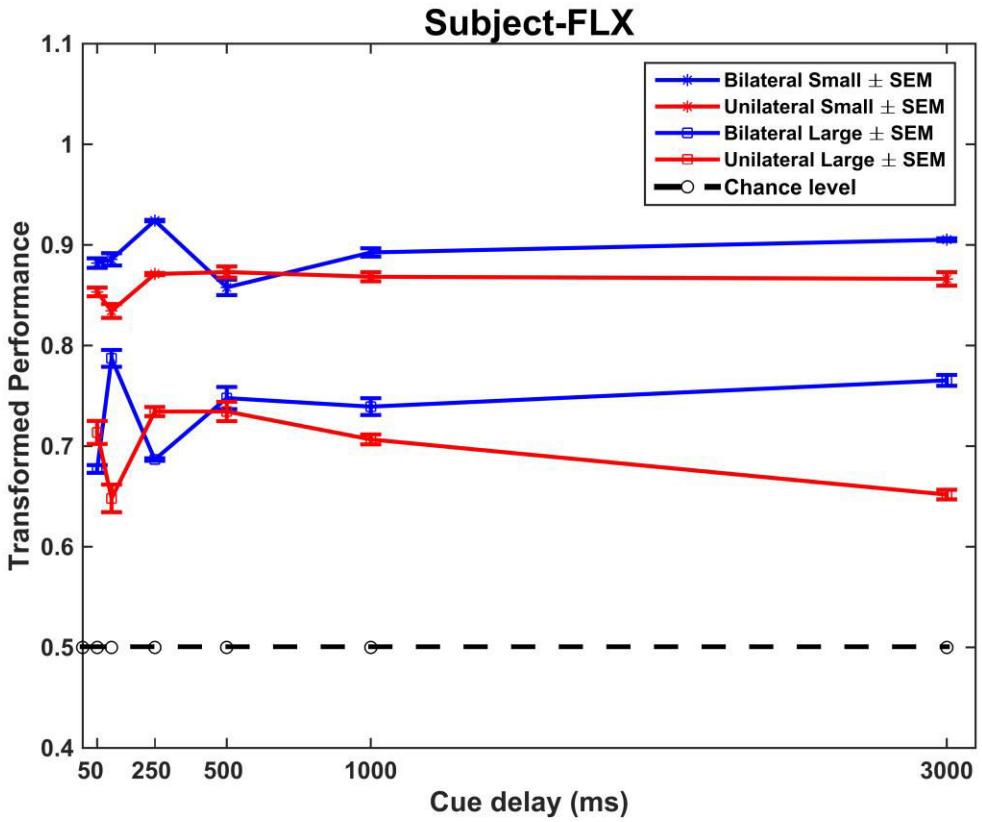

Figure. B.1. 3. Average transformed performance for unilateral small, unilateral large, bilateral small, and bilateral large set sizes for subject FLX.

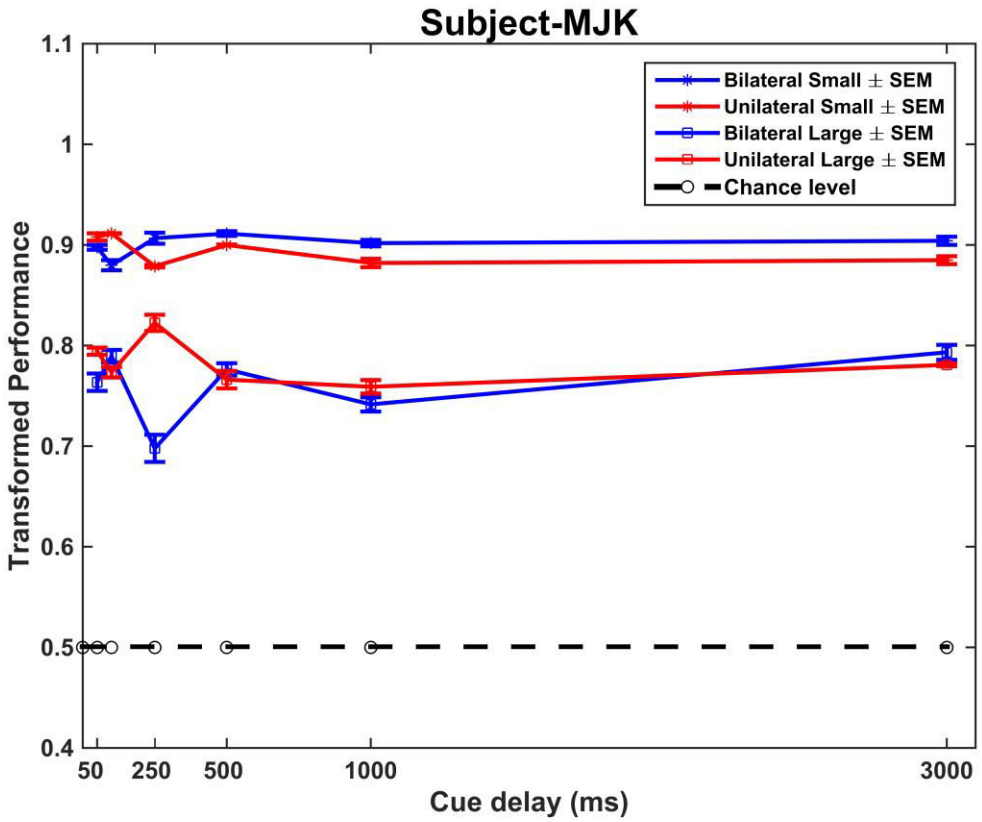

Figure. B.1. 4. Average transformed performance for unilateral small, unilateral large, bilateral small, and bilateral large set sizes for subject MJK.

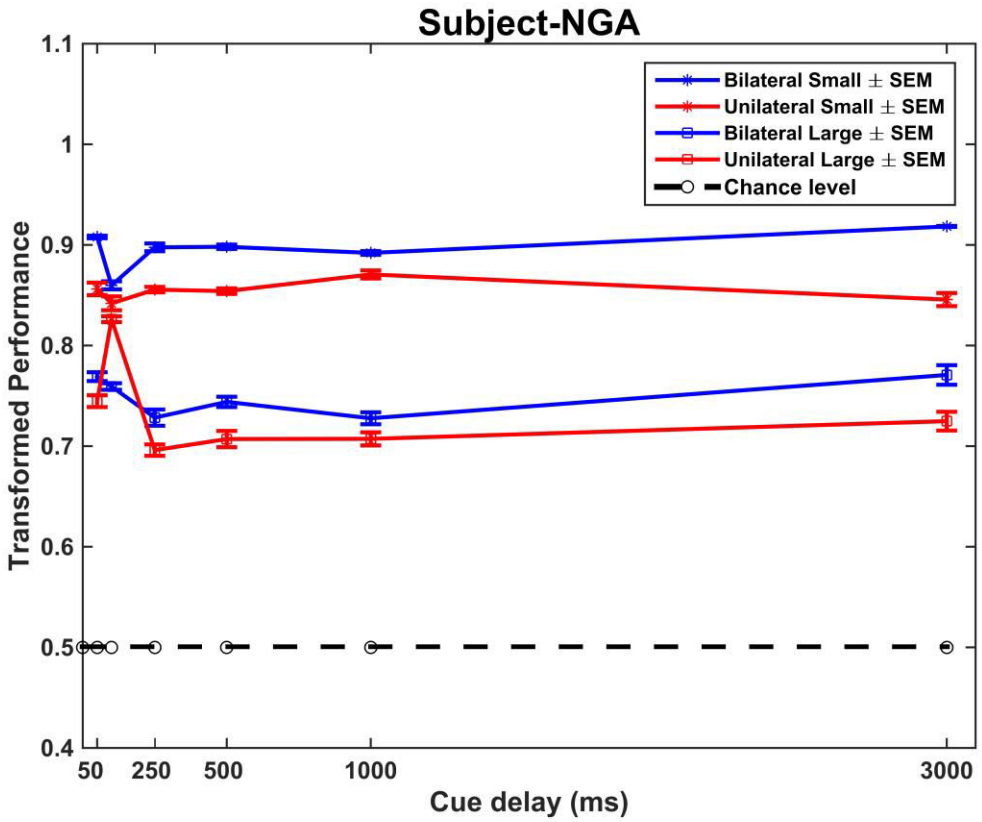

Figure.B.1. 5. Average transformed performance for unilateral small, unilateral large, bilateral small, and bilateral large set sizes for subject NGA.

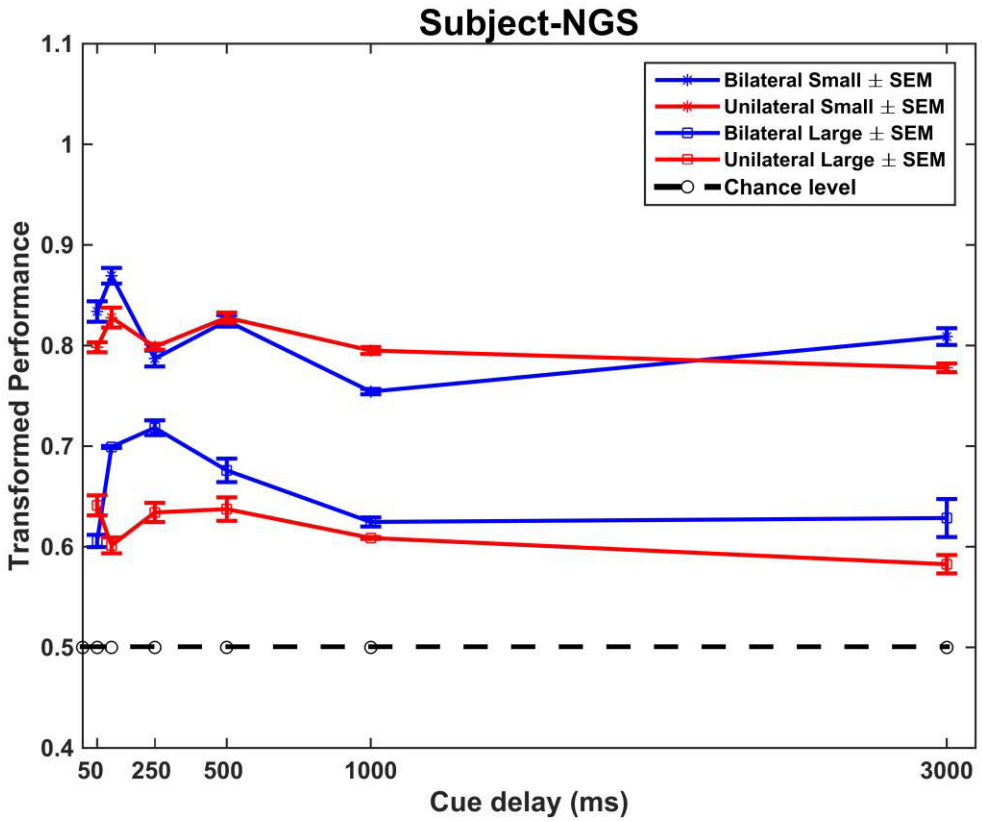

Figure B.1. 6. Average transformed performance for unilateral small, unilateral large, bilateral small, and bilateral large set sizes for subject NGS.

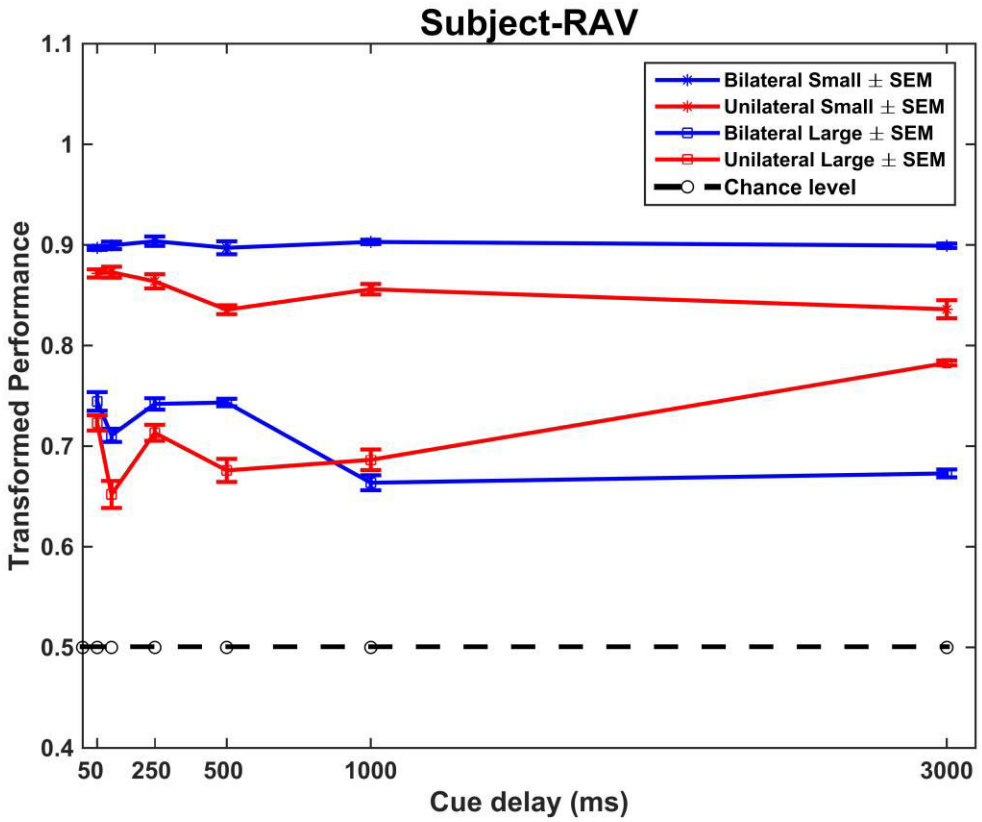

Figure B.1. 7. Average transformed performance for unilateral small, unilateral large, bilateral small, and bilateral large set sizes for subject RAV.

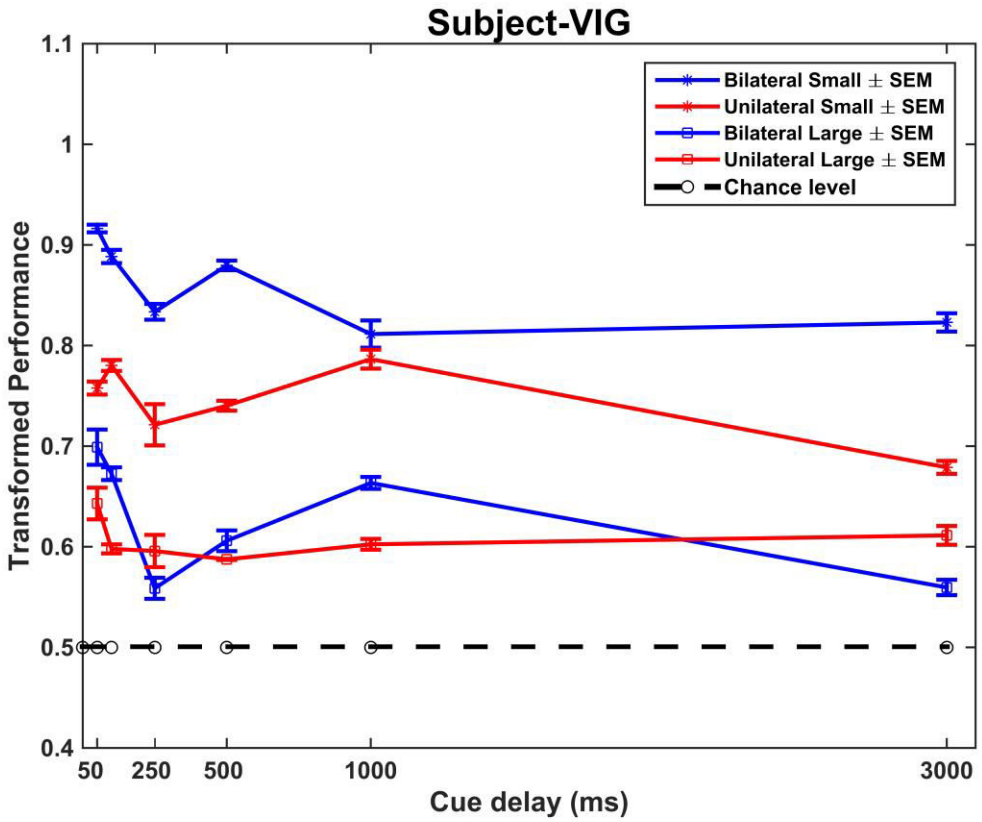

Figure B.1. 8. Average transformed performance for unilateral small, unilateral large, bilateral small, and bilateral large set sizes for subject VIG.

APPENDIX B

Appendix B.2. Subject NGS plot for set size = 6 in experiment II

Subject NGS did experiment 2 with set size = 6 and replicated experiment II reported in Huynh et al., (2015). Transformed performance for the unilateral and bilateral conditions are plotted in red and blue, respectively. This subject's performance for the conditions used in Huynh et al. is plotted in cyan. Although the results from subject NGS replicated the findings reported on Huynh et al., there was no difference between the bilateral and the unilateral visual-field condition, consistent with my other findings. The drop in performance as a function of cue delay was between 3%-10% for the three conditions.

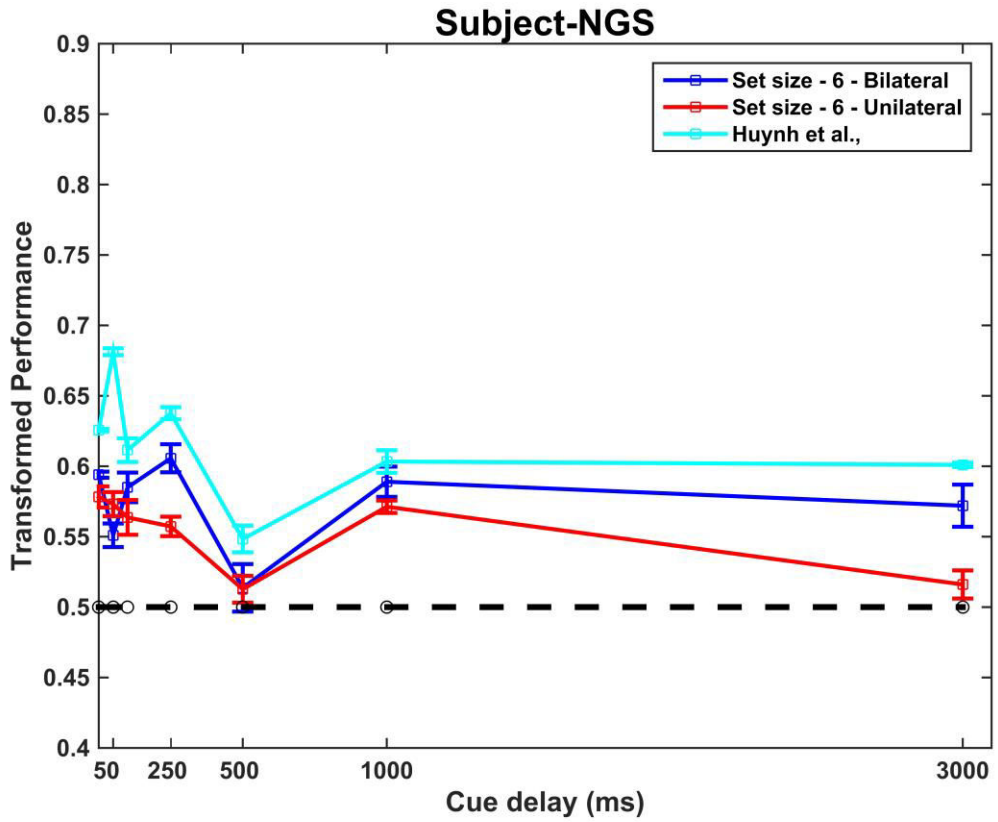

Figure B.2. 1. Average transformed performance of NGS for set size = 6 for unilateral and bilateral conditions. Plot also has replication of Huynh et al., study

APPENDIX C

Appendix C.1 Individual Subjects' (N=3) plots for experiment III- Pilot data

Percentage correct for each subject for the unilateral and bilateral conditions for two and four targets: Set Size = 8

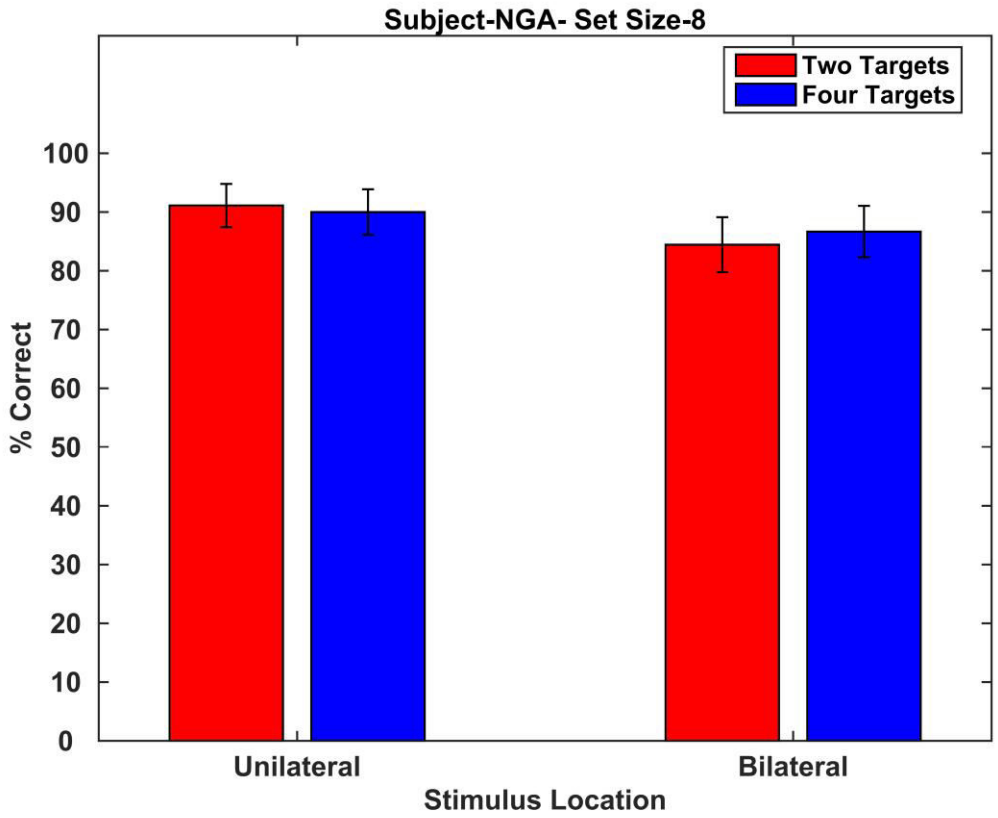

Figure C.1. 1. Percent correct for subject NGA for the unilateral and bilateral conditions for two and four targets for set size = 8.

SUBJECT-NGA	Average % Correct-Unilateral	% Correct-Unilateral-SEM	Average % Correct-Bilateral	% Correct Bilateral-SEM
Two targets	91.11	3.68	84.44	4.68
Four targets	90.00	3.87	86.67	4.39

Table C.1. 1. Percent correct for subject NGA: Two and four targets unilateral condition and two and four targets bilateral condition.

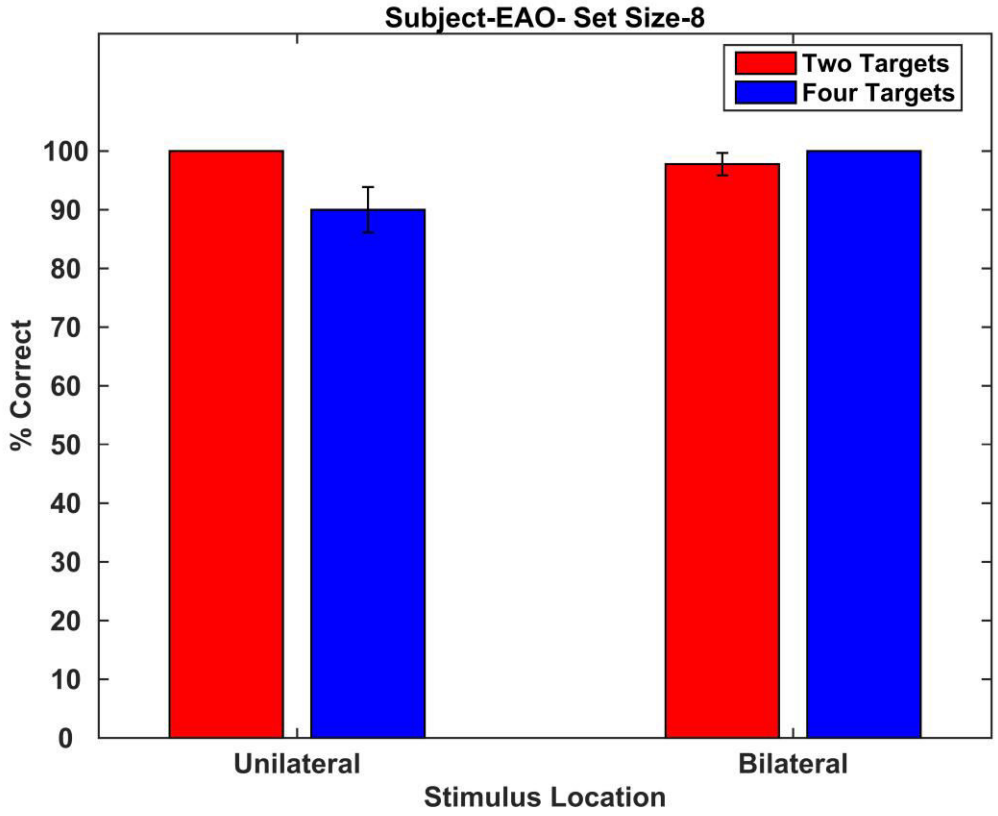

Figure C.1. 2. Percent correct for subject EAO for the unilateral and bilateral conditions for two and four targets for set size = 8.

SUBJECT-EAO	Average % Correct-Unilateral	% Correct-Unilateral-SEM	Average % Correct-Bilateral	% Correct Bilateral-SEM
Two targets	100.00	0.00	97.78	1.90
Four targets	90.00	3.87	100.00	0.00

Table C.1. 2. Percent correct for subject EAO: Two and four targets unilateral condition and two and four targets bilateral condition.

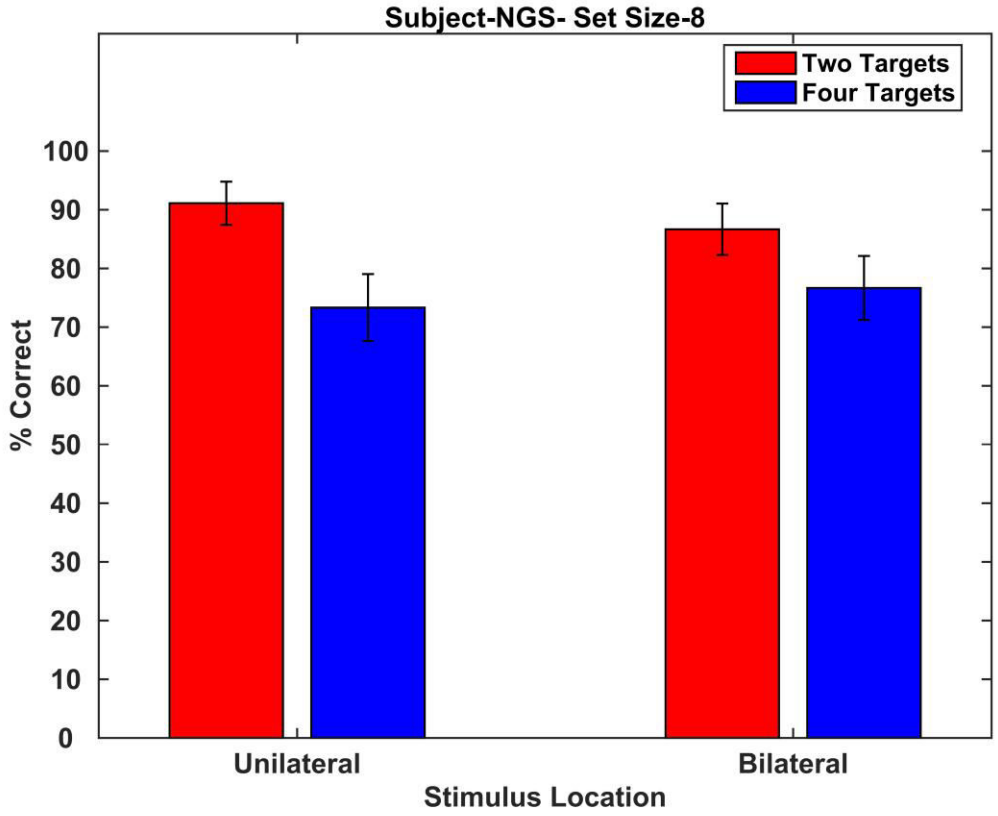

Figure C.1. 3. Percent correct for subject NGS for the unilateral and bilateral conditions for two and four targets for set size = 8.

SUBJECT-NGS	Average % Correct-Unilateral	% Correct-Unilateral-SEM	Average % Correct-Bilateral	% Correct Bilateral-SEM
Two targets	91.11	3.67	86.67	4.39
Four targets	73.33	5.71	76.67	5.55

Table C.1. 3. Percent correct for subject NGS: Two and four targets unilateral condition and two and four targets bilateral condition.

Appendix C.2 Average performance plot for three subjects experiment 3 - Pilot data

Percentage correct for unilateral and bilateral conditions for two and four targets:

Set Size = 8

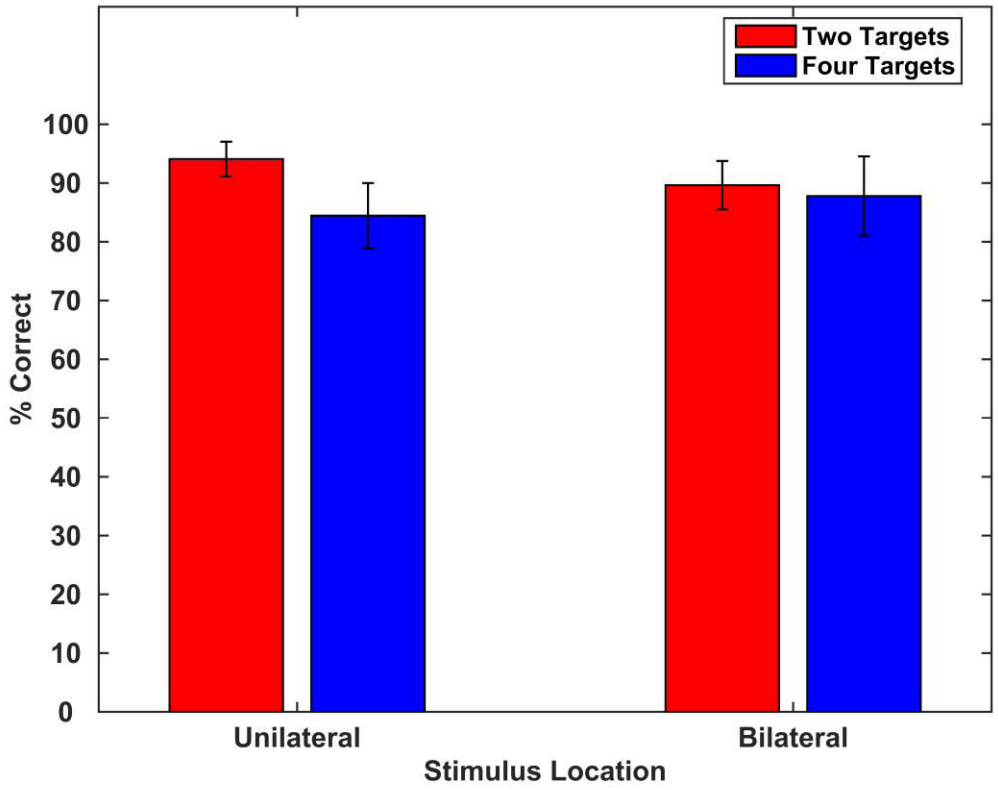

Figure. C.2. 1. Average percent correct for all subjects (N=3) for the unilateral and bilateral conditions for two and four targets for set size = 8.

Targets	Average % correct-Unilateral	% correct-Unilateral-SEM	Average % correct-Bilateral	% correct-Bilateral-SEM
Two	94.07	2.96	89.63	4.12
Four	84.44	5.56	87.79	6.76

Table.C.2. 1. Average percent correct for all subjects (N=3) for the unilateral and bilateral conditions for two and four targets for set size = 8.

From Appendix C.1 and C.2, the performance of the subjects for set size = 8 in the unilateral two-target condition was better than the bilateral two-target condition. The performance for the bilateral four-target condition was better than the unilateral four-target condition.

Appendix C.3 Individual Subjects' (N=8) plots for experiment 3

Percentage correct for each subject for the unilateral and bilateral conditions for two and four targets: Set Size = 10

Appendix C.3 consists of individual plots for each subject for the unilateral and bilateral conditions for two and four targets. From the figures in this appendix, performance in the bilateral and unilateral visual-field conditions were the same for two and four targets, expect for subject VIG.

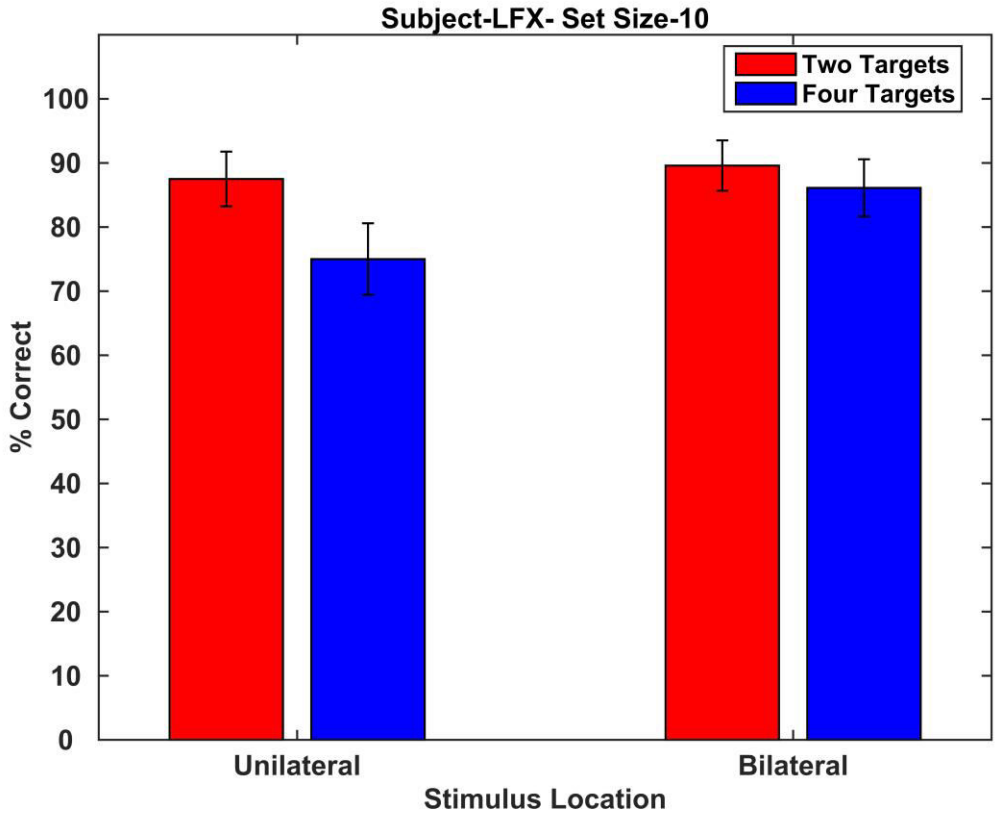

Figure.C.3. 1. Percent correct for subject LFX for the unilateral and bilateral conditions for two and four targets for set size = 10.

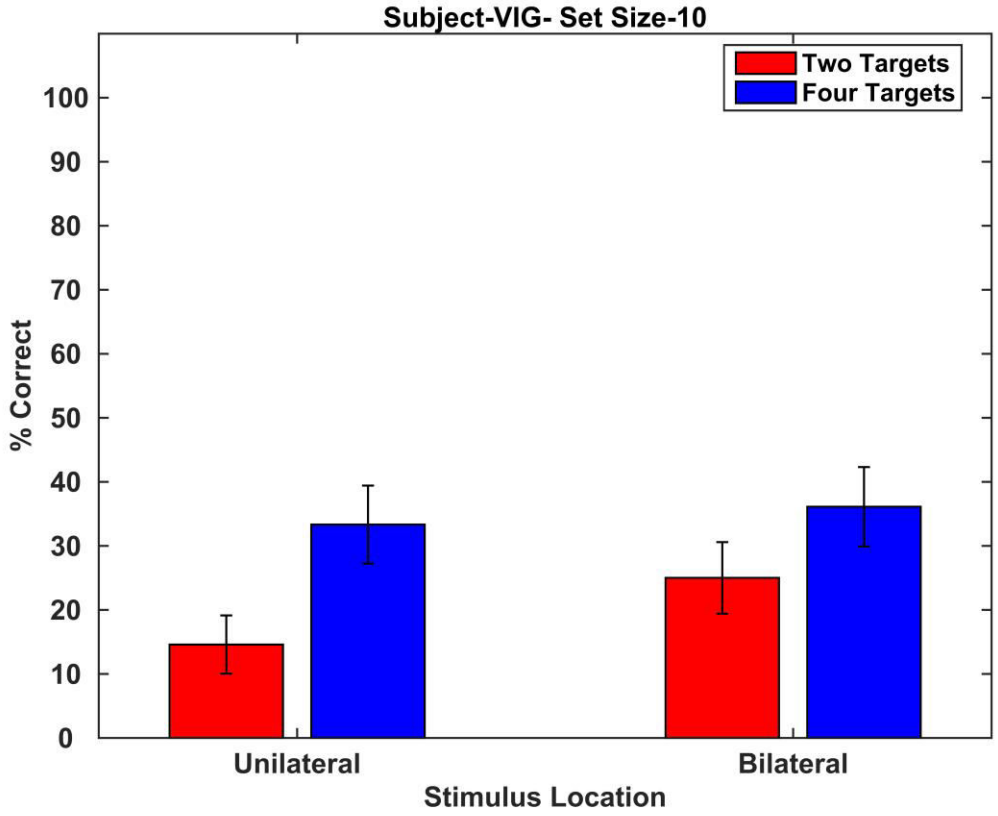

Figure.C.3. 2. Percent correct for subject VIG for the unilateral and bilateral conditions for two and four targets for set size = 10.

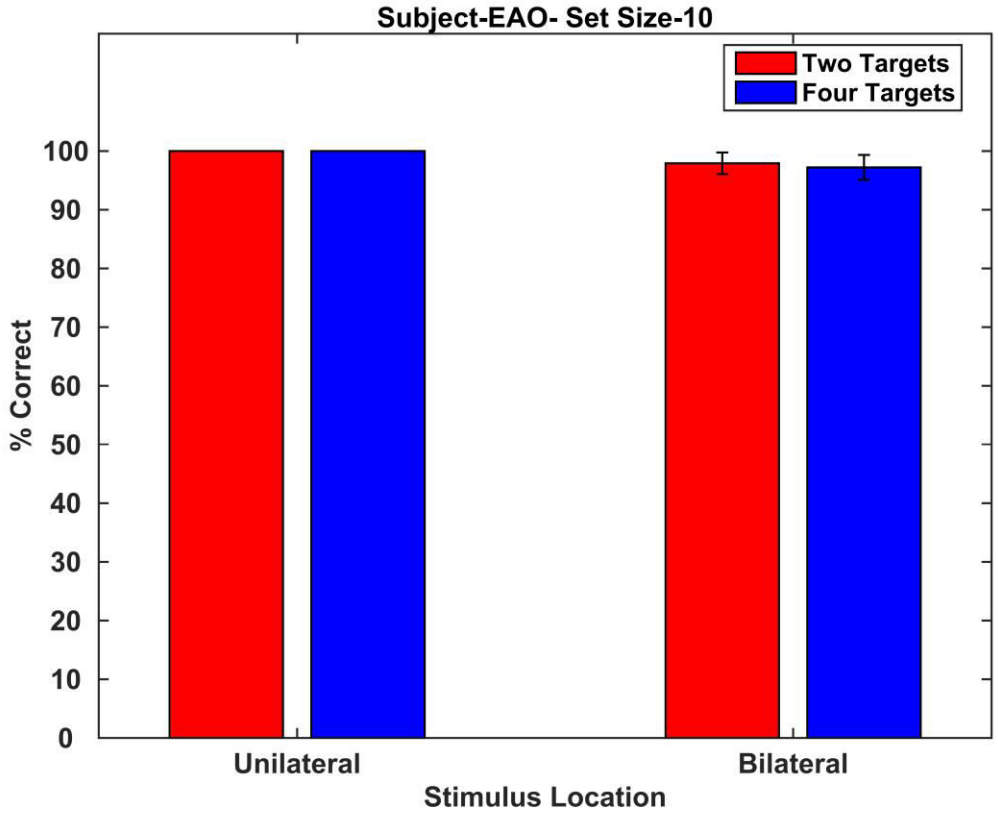

Figure.C.3. 3. Percent correct for subject EAO for the unilateral and bilateral conditions for two and four targets for set size = 10.

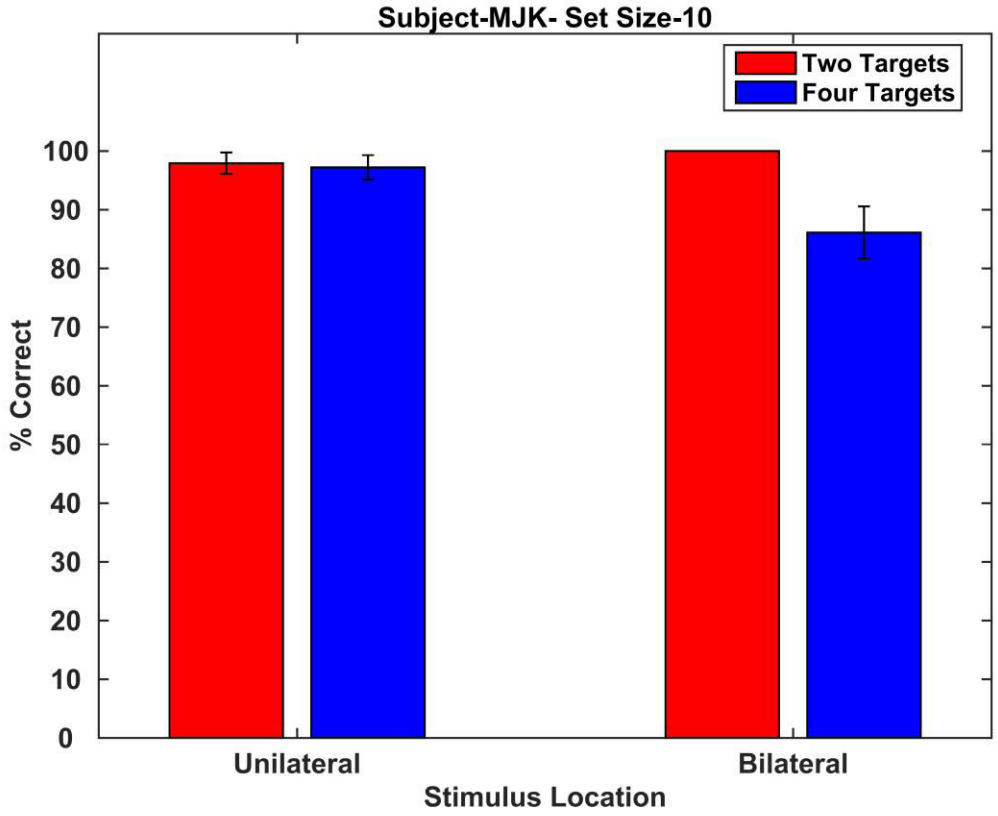

Figure.C.3. 4. Percent correct for subject MJK for the unilateral and bilateral conditions for two and four targets for set size = 10.

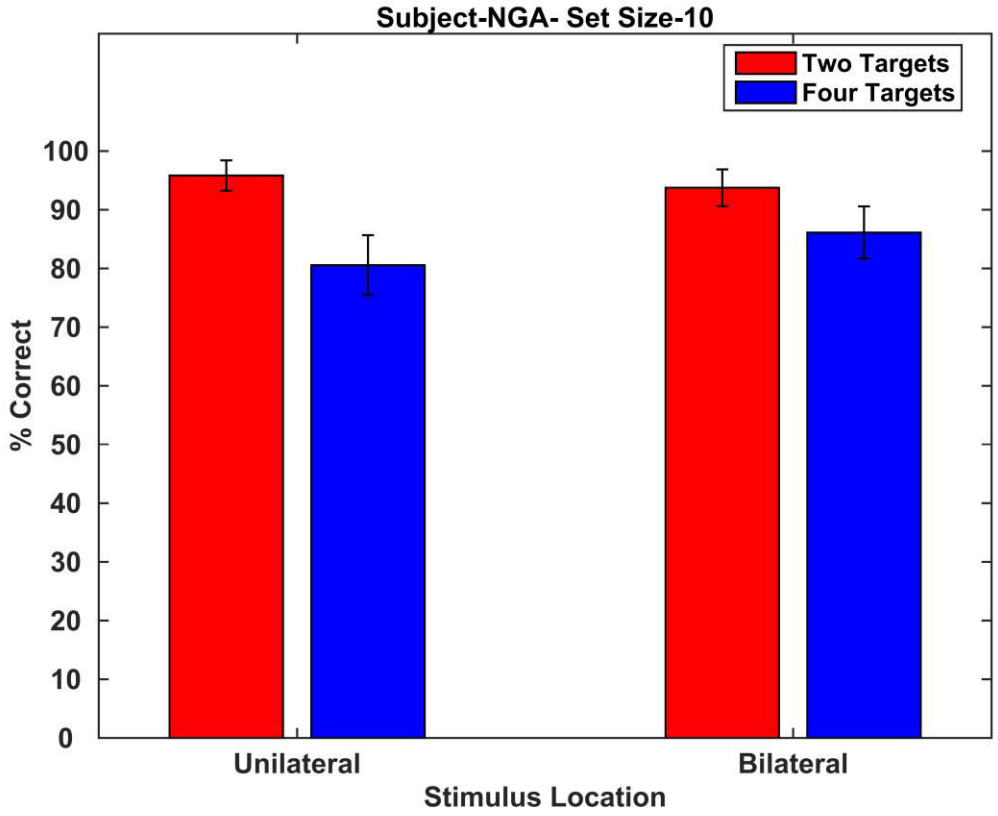

Figure.C.3. 5. Percent correct for subject NGA for the unilateral and bilateral conditions for two and four targets for set size = 10.

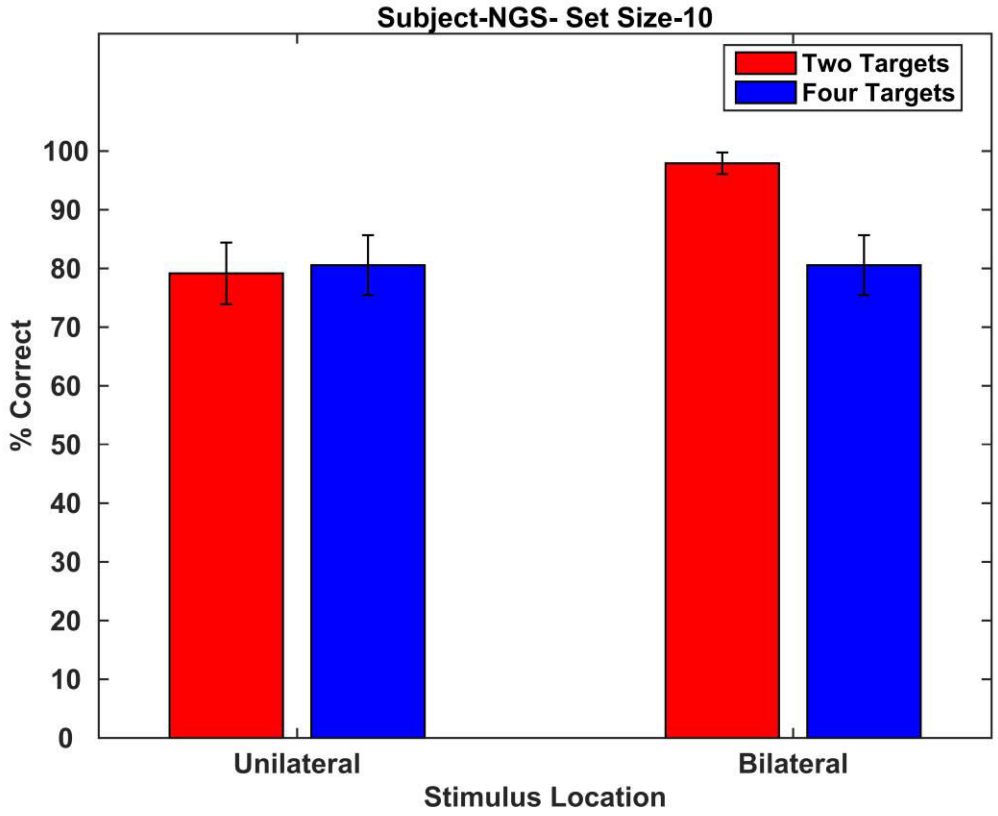

Figure.C.3. 6 Percent correct for subject NGS for the unilateral and bilateral conditions for two and four targets for set size = 10.

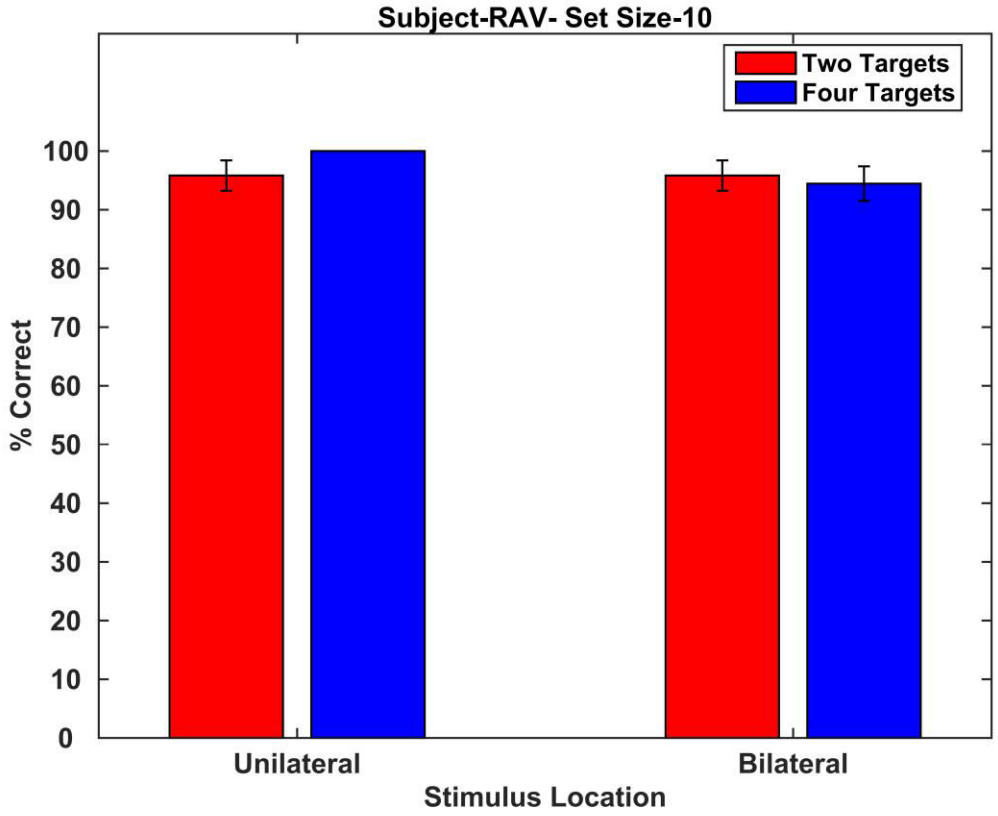

Figure.C.3. 7. Percent correct for subject RAV for the unilateral and bilateral conditions for two and four targets for set size = 10.

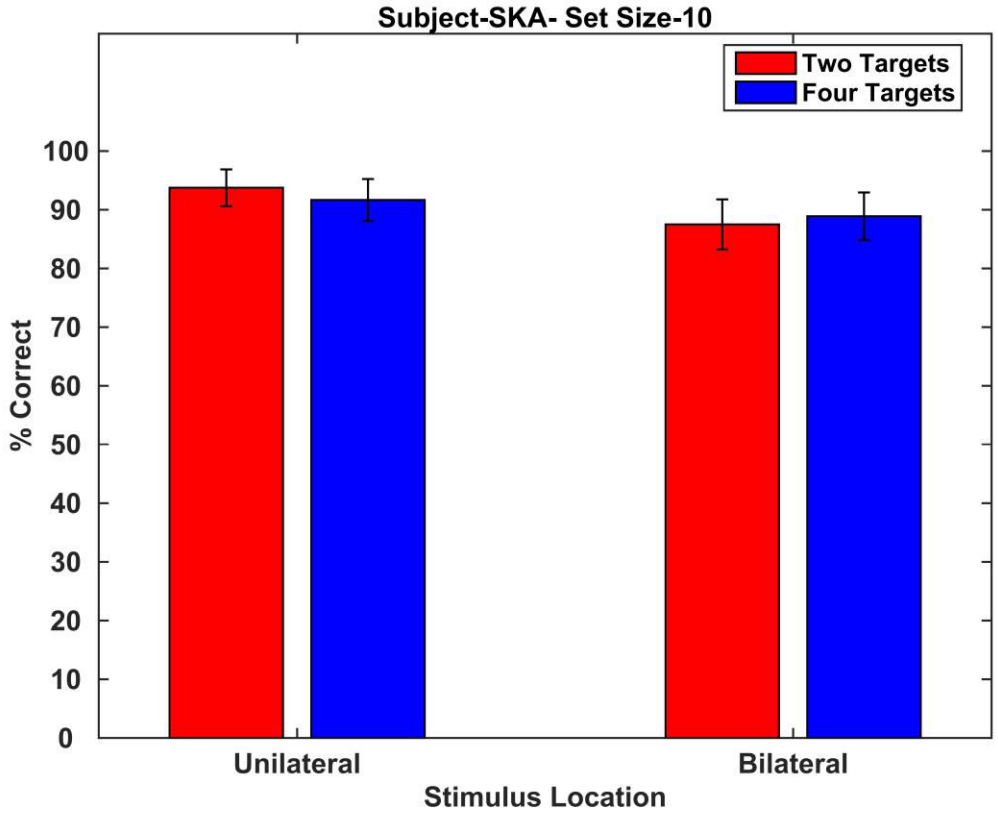

Figure.C.3. 8. Percent correct for subject SKA for the unilateral and bilateral conditions for two and four targets for set size = 10.